COEVOLUTIONARY PATTERNS IN CENTRAL AMERICAN BIGNONIACEAE[1]

Alwyn H. Gentry[2]

The 600 species of the family Bignoniaceae are mostly large-flowered, wind-dispersed, woody, tropical plants. Division of the family into three major tribes —Tecomeae, Bignonieae, and Crescentieae—is based primarily on fruit morphology. In the neotropics the majority of the species are lianas, virtually all belonging to the Bignonieae. The neotropical Tecomeae and Crescentieae (excluding *Schlegelia*) are arborescent.

Bignoniaceae is one of the most important families of woody plants and the most important family of lianas in the Central American forest ecosystems I have studied. This is true no matter whether diversity, frequency of occurrence, or density is chosen as an index of importance (Gentry, 1972, and in preparation). The coevolutionary patterns found in such an important family are clearly very important to understanding the evolution of the adaptive strategies of the animals which interact with these plants. Several aspects of bignon biology indicate long histories of coevolution with various groups of animals. I will note separately some evolutionary diversifications in the family related to interactions with herbivores, frugivores, and pollinators.

VEGETATIVE INTERACTIONS

Non-reproductive interactions of bignons with animals have led to the development of different kinds of defensive mechanisms against herbivores. Chemical defenses in the Bignoniaceae appear to be very effective. In the field the level of herbivore damage to bignons is generally low, and even when dried plants of this family are remarkably resistant to insects (Lewis, 1971). The wood of this family is much prized for construction because of its great durability. Beams of *Tabebuia* wood, known to have been exposed to the elements for 400 years, are still free of decay (Record & Hess, 1940). *Tabebuia guayacan* is one of the most durable woods of Panama with respect to terrestrial organisms, and the few sound trees remaining from the forest inundated over 50 years ago by Gatun Lake are mostly *T. guayacan* (Southwell & Bultman, 1971). Resistance to herbivores and wood-destroying insects is related to the presence of large quantities of lapachol in many species of the family (Sandermann & Dietrichs, 1957; Gentry, 1967). Other genera are presumably protected by such unidentified chemical

---

[1] This paper is based on a section of a Ph.D. dissertation submitted to the graduate school of Washington University of St. Louis. I would like to thank John Dwyer, Walter Lewis, Alan Covich, Owen Sexton, Thomas Croat, Robert Colwell, Dan Janzen, Herbert Baker, and others for useful comments on earlier versions of the manuscript; Peter Raven's criticisms of the final version were especially helpful. Robert Dressler assisted greatly with identification of pollinators. Support for this study was provided by a National Science Foundation graduate fellowship, an NSF predoctoral dissertation improvement grant (GB-28496), and NSF grant GB-40103.

[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

Ann. Missouri Bot. Gard. 61: 728–759. 1974.

compounds as those associated with the strong onion or garlic odor of *Pachyptera* (*Pseudocalymma*) and the clove odor of *Tynnanthus. Tanaecium* is characterized by a strong almond (cyanide) odor and has been responsible for livestock poisoning in Colombia (Dugand, 1942). Yet despite the general effectiveness of their chemical defenses, bignons are host to such specialized herbivores as leaf-mining beetles of the buprestid genus *Hylaeogena.* Of the about 15 species of *Hylaeogena* known from Panama, all but one feed on various bignon lianas (Hespenheide, personal communication).

Most bignon species have a second system of protection from herbivores: ants. The presence of ants on a plant has been shown to be an effective deterrent to herbivores (Janzen, 1967*b*, 1972), and many bignons have specialized mechanisms for ant attraction. The large-pithed twigs of many Tecomeae are easily hollowed out and inhabited by ants. In Central America *Tabebuia palustris, T. rosea, Godmania aesculifolia,* and *Jacaranda copaia* often host ant colonies inside their twigs. The name *Tabebuia* was based upon the Tupian Indian words meaning "ant" and "wood" and refers to this phenomenon in some species of that genus. Most of the lianas of the Bignonieae attract ants through production of sugary secretions. In specialized species well defined secretory glands are concentrated at the nodes of young branchlets and sometimes at the petiole apex. Small ants regularly cluster around these glandular areas. Even in many species without discrete glands ants congregate at the nodes of young branches, where a sticky substance is produced. In general, species which attract ants through sugar-secreting glands (many Bignonieae) appear to be more advanced than those which attract them through easily-hollowed twigs (Tecomeae).

Coevolution and Seed Dispersal

Tribal division in the Bignoniaceae is largely based on fruit morphology (Fig. 1). The Tecomeae have capsules dehiscing perpendicular to the septum. The more advanced Bignonieae have capsules dehiscing parallel to the septum and (in the New World) a specialized replum. Seeds of both Tecomeae and Bignonieae are mostly winged and wind dispersed. Such minor tribes as Tourrettieae and Eccremocarpeae also have dehiscent capsules and winged seeds. The third important tribe, Crescentieae, has indehiscent fruits.

The differences in fruit morphology between the Crescentieae and the rest of the family are so pronounced that some authors (*e.g.* Lindley, 1847; Seemann, 1860) proposed their segregation as a separate family. However, an understanding of their seed dispersal ecology indicates that the Crescentieae are closely related to the Tecomeae (Fig. 2). The indehiscent fruit of Crescentieae is derived from the dehiscent fruit of Tecomeae through coevolution with frugivorous mammals.

Parmentiera is the non-missing link which provides the clues needed to understand the phylogeny of the Crescentieae. The fruits of *Parmentiera cereifera,* though fleshy and indehiscent, are superficially very similar to young fruits of *Tabebuia* and other *Tecomeae.* They have exactly the elongate-linear form of *Tabebuia* fruit; more significantly, the seeds are vestigially winged. The very

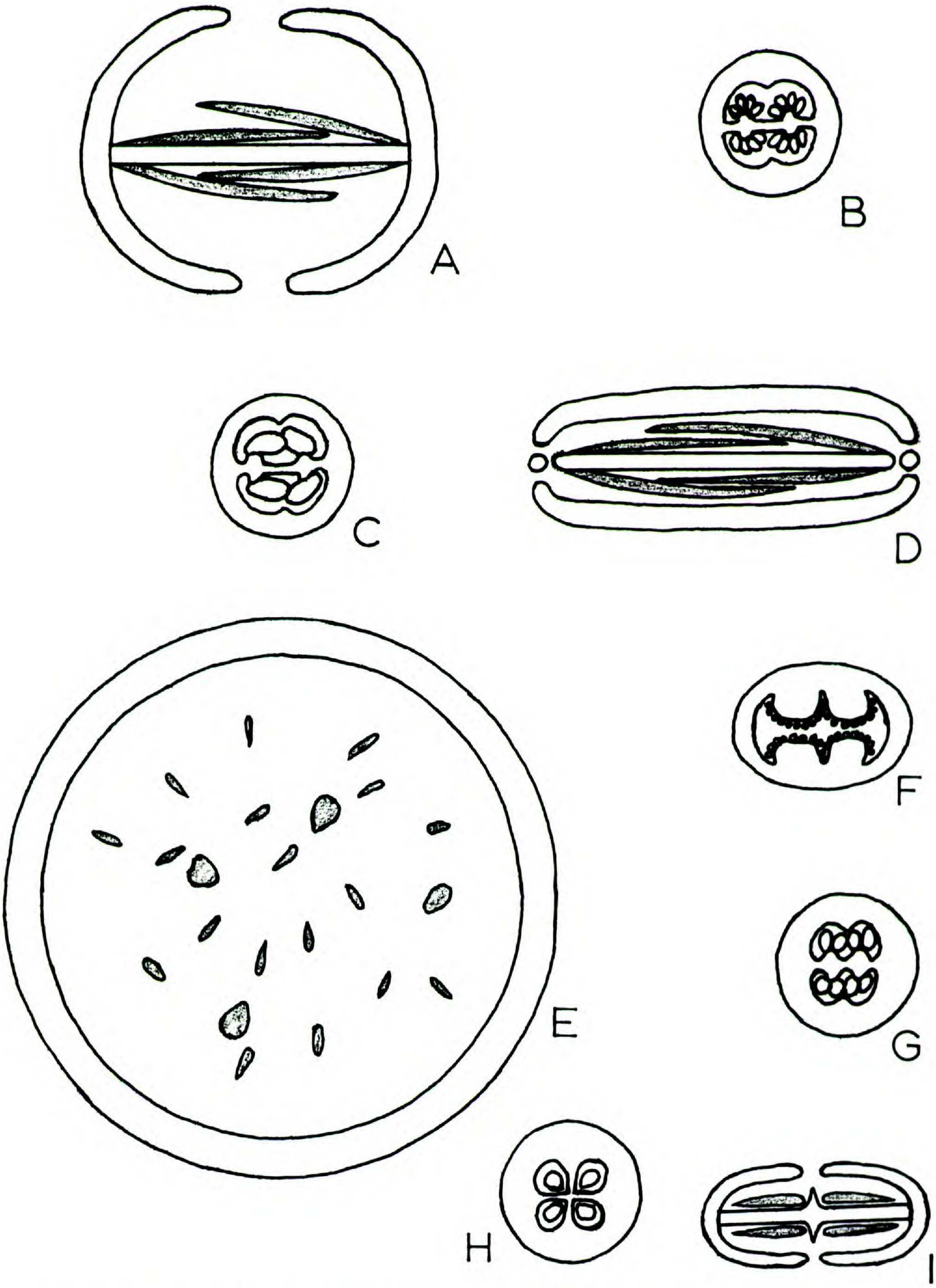


FIGURE 1. Fruit and ovary cross sections of Bignoniaceae (schematic).—A. Tecomeae fruit.—B. Tecomeae ovary.—C. Bignonieae ovary.—D. Bignonieae fruit.—E. Crescentieae fruit.—F–G. Crescentieae ovary.—H. Tourrettieae ovary.—I. Tourrettieae fruit.

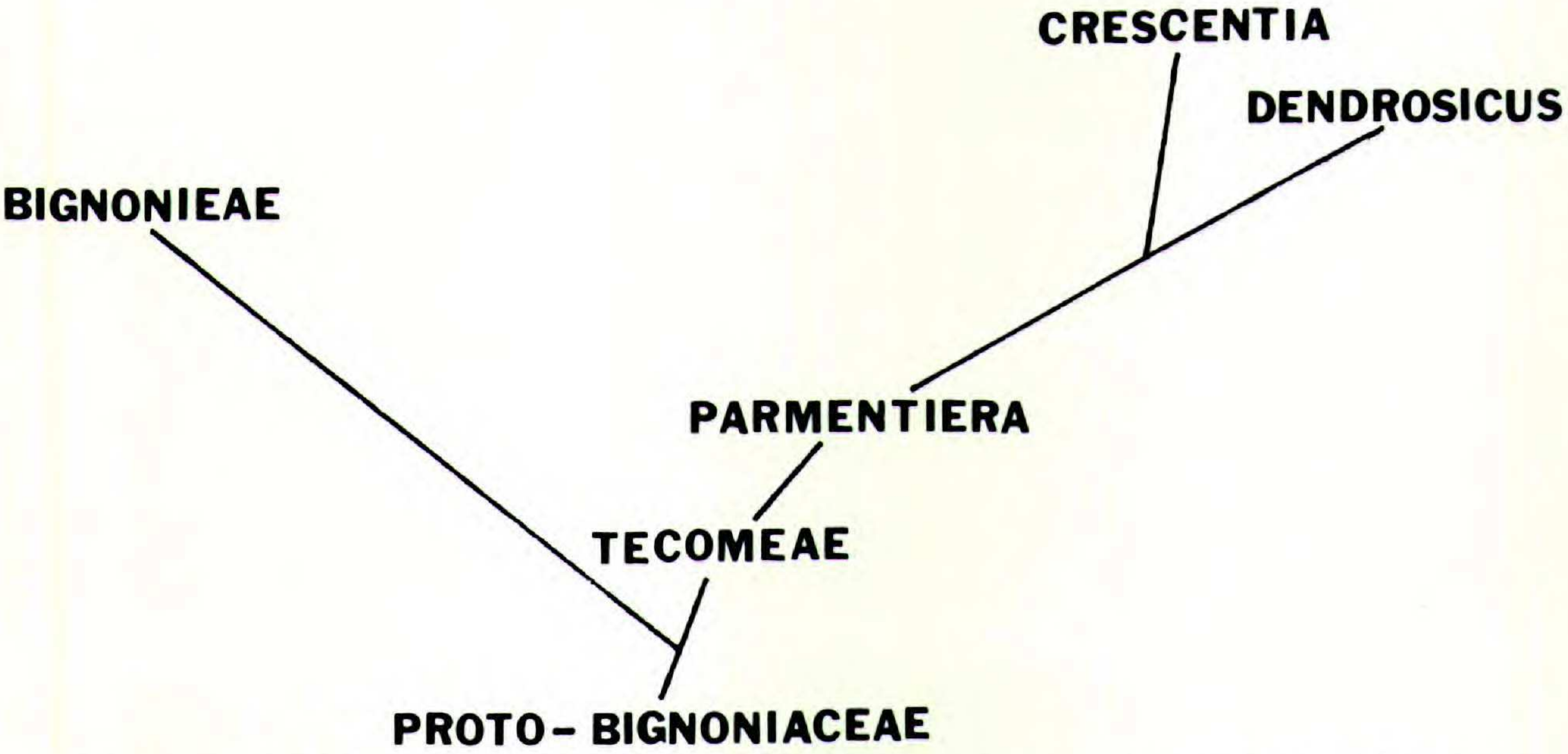


FIGURE 2. Phylogenetic relationships of the New World Crescentieae (*Parmentiera, Dendrosicus,* and *Crescentia*).

small seeds of *Parmentiera* are quite like immature *Tabebuia* seeds. It seems evident that *Parmentiera* has indeed been derived from a species of Tecomeae or proto-Tecomeae with dehiscent fruit and winged seeds.

It might be argued that it would be difficult for a species to make the critical change from dehiscent to indehiscent fruits, but an acceptable mechanism is readily available. It is well known that monkeys are extremely destructive of young fruits; I have seen most of the green fruits of a tree of *Tabebuia guayacan* stripped off by a troop of howler monkeys on Barro Colorado Island. Although some wind-dispersed plants cope with monkeys and other frugivorous mammals and birds by developing thickened or spiny fruits, an alternate evolutionary solution takes advantage of attraction of fleshy young fruits to frugivores and utilizes these animals as dispersal vectors. Neotenous maturation of seeds and selection for fleshier more edible fruits would lead from the dehiscent Tecomeae fruit to the fruit of *Parmentiera* with no evolutionarily awkward inadaptive gap. The succulent pulp of these fruits is avidly eaten by many mammals and they are often fed to cattle in Central America (Seemann, 1854; Standley, 1928). The central part of the *Parmentiera* fruit is fibrous-fleshy, and the seeds are situated between this core and the fleshy pericarp. Often the seeds and core remain uneaten. Probably the small mucilaginous seeds can also pass unharmed through a mammalian digestive system.

Other genera of New World Crescentieae have spherical or ellipsoid fruits with hard shells surrounding a soft pulp in which the seeds are embedded. The pulp is eaten by mammals and in some species by man. A series of additional evolutionary steps could easily produce these fruits from those of *Parmentiera*. Shortening and thickening of the fruit involves relatively little change and has taken place in such species of *Parmentiera* as *P. macrophylla* and *P. aculeata* (H.B.K.) Seem. I visualize *Dendrosicus* (*Enallagma*) and *Crescentia* as having developed the hard exocarps usually thought of as characteristic of the Crescentieae as a protection for the immature fleshy fruits. Most species of *Dendrosicus* are montane, and the fruit shell is relatively soft. However such protective exocarps would also make possible long distance dispersal of the whole fruit by water. Water dispersal would in turn select for harder, thicker exocarps; and the fruits of water-dispersed *Dendrosicus latifolius* have the hardest and thickest exocarps of the genus. This species is a well known plant occurring along sea coasts throughout the Caribbean region and also along the Pacific coast of Central America and Colombia. Its fruits are frequently found cast upon the beach, often with still viable seeds. The fruit of this speices is also eaten by mammals, notably pacas, and a balance appears to have been achieved whereby long distance dispersal of the fruit is by water and local dispersal of the seed by frugivores.

Crescentia must have evolved in a similar manner. I have seen apparently naturalized (possibly native?) trees of *Crescentia cujete* along the Caribbean coast of Costa Rica in an uninhabited swampy area south of Cauhita and have found occasional fruits with viable seeds cast up on the beach. *Crescentia amazonica* Ducke, which grows along the banks of the Amazon and Orinoco, is surely water-dispersed. Even the savannah species *C. alata* H.B.K. is readily dispersed during the rainy season in Guanacaste, Costa Rica, when the poorly drained savannahs often stand in water after a heavy rain. The fruits float, and naturally dispersed juvenile plants are relatively common along sandbars where the fruits are cast up by flood waters. The pulp of *Crescentia* is also eaten by mammals so that this genus, too, has a supplementary method of seed dispersal.

Schlegelia, a genus of lianas with mostly bird-dispersed fruits, has usually been included in the Crescentieae but is excluded from this discussion. It is only distantly related and may belong in the Scrophulariaceae.

An interesting sidelight to this story is the correlation between mammal dispersal and endemism in the Bignoniaceae. Wind-dispersed and water-dispersed species of *Tecomeae* and *Bignonieae* are typically wide-ranging, many occurring from Mexico to Argentina (Gentry, in preparation). The species of Crescentieae with chiefly water-dispersed fruits likewise have wide ranges—*Dendrosicus latifolius* from Mexico to Venezuela and Pacific Colombia and throughout the West Indies, *Crescentia amazonica* the length of the Amazon and Orinoco, *C. alata* from Mexico to Costa Rica, *C. cujete* throughout tropical America through the intervention of man, although its natural range is obscure. However the primarily mammal-dispersed species of Crescentieae tend to be highly endemic with very restricted ranges. Of the wind- and water-dispersed Panamanian–Costa Rican species of Bignoniaceae, 78% reach Venezuela (Gentry, Bignoniaceae in *Flora of Venezuela*, in preparation; several more species are to be expected) and 73% the Maya area (Seibert, 1940; Standley & Williams, 1974). None of the 7 exclusively animal-dispersed Costa Rican–Panamanian species reaches either the Maya area or Venezuela. Nor do any of the 9 animal-dispersed species of the Maya area reach Costa Rica or Panama. In fact none of the *ca.* 18 species of animal-dispersed Central American Crescentieae is found in more than two adjacent countries. Apparently animal dispersal in the Bignoniaceae occurs on a much more local basis than wind or water dispersal, and this has resulted in a prevalence of local species among animal-dispersed groups.

Pollination Ecology

The most intricate interactions of bignons with animals are related to pollination ecology. Adaptations in floral morphology, flowering phenology, and seasonality are the raw materials which make possible the various pollination strategies of the different species of Bignoniaceae.

FLORAL MORPHOLOGY

The basic morphology of a bignon flower is represented in Figure 3A–D. The sepals are fused into a cupular calyx. The petals are fused into a tubular five-lobed corolla with two longitudinal folds in the floor of its tube. The part of the base of the tube which fits into the calyx is narrowed. The filaments of the four fertile stamens are fused to the corolla tube at the top of its narrower basal part. The filament bases and the corolla tube at the level of insertion are glandular pubescent. The filaments are bent so that the divaricate anthers are held together in two pairs in the roof of the tube with the thecae parallel to the axis of the flower. The two anterior stamens are longer, and their anthers are aligned in front of those of the posterior stamens. A fifth stamen is reduced to an inconspicuous posterior staminode. The ovary is within the calyx, and beneath it is a conspicuous nectar-producing disc. The style is held against the roof of the corolla tube with the stigma usually held just in front of the foremost pair of anthers.

The upper and lower lobes of the bilamellate stigma are spread apart in unpollinated flowers. When triggered by contact with a pollinator, the stigma lobes close. The reaction is not proof of pollination, since touching the inner surface of the stigma lobes with a stick or finger also causes them to close. However, lack of closing of the stigma lobes following the pollen-collecting activities of some kinds of flower visitors indicates that they have not come in contact with the stigma and can be used to rule them out as pollinators. The stigma is usually held in front of the anthers, with its receptive surface facing the mouth of the tube where pollen carried by an entering pollinator can readily lodge. When the pollinator backs out of the corolla covered with pollen from that flower, it only contacts the nonreceptive outer surface of the closed stigma.

There are at least eight major variations on this basic pattern among the 78 species of Bignoniaceae occurring naturally in Costa Rica and Panama (Table 1). Cultivated Old World species show two additional morphological types and are included here to point out similarities and differences with their New World counterparts. Observed pollinators of Bignoniaceae are closely correlated with the morphological types described above (Table 2). Each type of floral morphology has a distinctive pollinator spectrum with relatively little overlap.

ANEMOPAEGMA-TYPE.—Most species of bignon have a thin membranaceous corolla, an open mouth, and included anthers. I have termed this the *Anemopaegma*-type of morphology (Fig. 3A–F). There are many minor modifications

TABLE 1. Summary of floral morphology: comparison of morphology, phenology, and pollination syndrome by flower type and genus. ? = flowers not observed but presumed to belong here.

Flower Type	Pollination syndrome	Genus	Morphology	Associated phenology
Anemopaegma	Open-mouthed bee flowers	*Adenocalymma* *Anemopaegma* (See also Table 2)	Medium-sized, tubular-campanulate, thin-thick textured, throat ridges smaller, tube little compressed, color various	Type 2, 3, and 4
Tynnanthus	Bee/butterfly flowers	*Ar. florida* *Godmania* *Mussatia* *Tynnanthus*	Small, anthers subexserted, often bilabiate, mouth open, lobes reduced, color various	Type 3
Pithecoctenium	Xylocopid flowers	*Ceratophytum* *Distictella* *Paragonia* *Pithecoctenium*	Medium-sized, tubular-campanulate, thick textured, throat ridges reduced, tube not compressed, mouth open, color various	Type 3 (2)
Amphilophium	Pseudocleistogamous flowers	*Amphilophium*	Very bilabiate, mouth closed by fused lobes, very thick, without throat ridges, purple	Type 2
Cydista	Dorsally compressed bee flowers	*Phryganocydia* *Cydista* *Clytostoma* *Scobinaria* *Tabebuia* (pro parte)	Medium-sized, tubular-infundibuliform, usually thin, conspicuous throat ridges, tube compressed dorsally, often with nectar lines, color various	Mainly Type 5
Tanaecium	Hawkmoth flowers	*Tanaecium* *Tab. striata*?	Very long narrow corolla tube, thick texture, anthers subexserted, white	Type 3, but opens at night
Martinella	Hummingbird flowers	*Martinella* *Pyrostegia* *Tourrettia*?	Medium-sized, average texture, anthers sometimes exserted, tubular, deep violet/red orange	Type 3
Crescentia	New World bat flowers	*Crescentia* *Dendrosicus* *Parmentiera*	Medium-sized, thick textured, campanulate, cauliflorous, whitish	Type 1
Spathodea	Old World bird flowers	*Spathodea*	Large, thin, more or less exserted anthers, campanulate, orange red	Type 3
Kigelia	Old World bat flowers	*Haplophragma* *Kigelia*	Large, thick-textured, campanulate, exposed, dull-colored	Type 1

of floral morphology within this group. The flowers may be yellow, white, blue, or magenta, often with a contrastingly colored throat which may change in color after anthesis. The corolla may be variously pubescent, lepidote, or glabrous outside. Some species have relatively short, thin corollas. Others have longer, thicker-textured corollas. All are conspicuous, fragrant, and produce nectar.

TABLE 2. Panamanian species of Bignoniaceae with floral morphology, phenology, and observed visitors. Visitors include nonpollinators as interpreted in text for each type of floral morphology and phenology. Most observations of visitors published elsewhere or mentioned in text are omitted. Most species with recorded visitors were observed for from 1 to 5 hours; other species were mostly observed sporadically for from 15 minutes to an hour. Three species were not seen in the field at all and 4 others were not seen in flower as noted under the "visitors" column. Visitors include those observed in Costa Rica, Belize and South America; phenological observations were made in Panama and Ecuador.

	Morphological type	Phenological type	Observed visitors
BIGNONIEAE			
Adenocalymma apurense (H.B.K.) Sandw.	Anem.	3(2)	—
A. arthropetiolatum A. Gentry	Anem.	3	—
Amphilophium paniculatum (L.) H.B.K.	Amph.	2	see text
A. pannosum (DC.) Bur. & Schum.	Amph.	2	—
Anemopaegma chrysanthum Dugand	Anem.	2	—
A. chrysoleucum (H.B.K.) Sandw.	Anem.	2	—
A. orbiculatum (Jacq.) DC.	Anem.	5	Halictids, xylocopids, *Euglossa igniventris*
A. puberulum (Seib.) Miranda	Anem.	?	not seen
A. santa-ritense A. Gentry	Anem.	2	—
Arrabidaea candicans (L. Rich.) DC.	Anem.	3	Halictids, trigonids, skippers, small anthophorids
A. chica (H. & B.) Verl.	Anem.	3	see text
A. conjugata (Vell.) Mart.	Anem.	3	Anthophorids, skippers
A. corallina (Jacq.) Sandw.	Anem.	3	Anthophorids
A. mollissima (H.B.K.) Bur. & Schum.	Anem.	3	Anthophorids
A. florida DC.	Tynn.	3	see text
A. pubescens (L.) A. Gentry	Anem.	3	trigonids, *Eulaema*, skippers, *Xylocopa*
A. patellifera (Schlecht.) Sandw.	Anem.	3	see text
Callichlamys latifolia (L. Rich.) Schum.	Anem.	3?	halictids, trigonids, 6 euglossine spp.
Ceratophytum tetragonolobum (Jacq.) Spr. & Sandw.	Pith.	2	—
Clytostoma binatum (Thunb.) Sandw.	Cyd.	5	—
Cuspidaria floribunda (DC.) A. Gentry	Anem.	3?	not seen
Cydista aequinoctialis (L.) Miers	Cyd.	5	see text
C. diversifolia (H.B.K.) Miers	Cyd.	5	see Gentry (1974)
C. heterophylla Seib.	Cyd.	4(5)	—
Distictella magnoliifolia (H.B.K.) Sandw.	Pith.	2?	not seen in flower
Lundia corymbifera (Vahl) Sandw.	Anem.	3	small moth
L. puberula Pittier	Anem.	3?	—
Macfadyena uncata (Andr.) Spr. & Sandw.	Anem.	2	—
M. unguis-cati (L.) A. Gentry	Anem.	4	anthophorids?
Martinella obovata (H.B.K.) Bur. & Schum.	Mart.	3	see text
Mussatia hyacinthina (Standl.) Sandw.	Tynn.	3	skippers, trigonids

TABLE 2. (continued)

	Morphological type	Phenological type	Observed visitors
Onohualcoa verrucifera (Schlecht.) A. Gentry	Anem.	4	—
Pachyptera hymenaea (DC.) A. Gentry	Anem.	3(4)	—
P. kerere (Aubl.) Sandw.	Anem.	2	bluish *Euglossa* sp.
P. parvifolia A. Gentry	Anem.	?	not seen in flower
P. standleyi (Steyerm.) A. Gentry	Mart.	3?	—
Paragonia pyramidata (L. Rich.) Bur.	Anem./ Pith.	3	Wasps, halictids, *Trigona*, *Melipona*, anthophorids, xylocopids. (also see text).
Phryganocydia corymbosa (Vent.) Bur. ex Schum.	Cyd.	5	see text and Gentry (1974)
P. phellosperma (Hemsl.) Sandw.	Cyd.	2	—
Pithecoctenium echinatum (Jacq.) Baill.	Pith.	2(3)	see text
Pleonotoma variabilis (Jacq.) Miers	Anem.	2	—
Scobinaria japurensis (DC.) Sandw.	Cyd.	3	see text
Stizophyllum inaequilaterum Bur. & Schum.	Anem.	2	—
S. riparium (H.B.K.) Sandw.	Anem.	2	*Euglossa* aff. *igniventris*, *Trigona* sp.
Tanaecium jaroba Sw.	Tan.	?	—
T. nocturnum (Barb. Rodr.) Bur. & Schum.	Tan.	3?	—
Tynnanthus croatianus A. Gentry	Tynn.	3	see text
Xylophragma seemannianum (Kuntze) Sandw.	Anem.	3	*Euglossa* sp., *E. townsendi*, large anthophorid.
TECOMEAE			
Godmania aesculifolia (H.B.K.) Standl.	Tynn. ?	3	halictids
Jacaranda copaia (Aubl.) D. Don	Anem.	3	—
J. caucana subsp. *sandwithiana* A. Gentry	Anem.	3	hummingbirds, medium-sized bees
Tabebuia chrysantha (Jacq.) Nichols.	Anem./ Cyd.	4	see Borrero (1972)
T. guayacan (Seem.) Hemsl.	Cyd./ Anem.	4	hummingbirds, medium-sized anthophorids
T. impetiginosa (Mart. ex DC.) Standl.	Anem.	4	anthophorids, trigonids, halictids, vespids, hummingbirds
T. ochracea subsp. *neochrysantha* (A. Gentry) A. Gentry	Anem./ Cyd.	4	several anthophorids, *Euglossa* sp., trigonids, halictids, wasps, hummingbirds.
T. palustris Hemsl.	Cyd./ Anem.	2	halictids
T. rosea (Bertol.) DC.	Anem./ Cyd.	3	*Xylocopa*, *Eulaema*, *Trigona*, small anthophorids
T. striata A. Gentry	prob. Tan.	?	not seen in flower.

TABLE 2. (continued)

	Morpho-logical type	Pheno-logical type	Observed visitors
CRESCENTIEAE			
Crescentia cujete L.	Cres.	1	see text
Dendrosicus isthmicus A. Gentry	Cres.	1(2)	—
D. kennedyi A. Gentry	Cres.	1(2)	not seen in flower
D. latifolius (Mill.) A. Gentry	Cres.	1(2)	unidentified bats (not seen to enter flower)
D. sessilifolia (Donn. Sm.) A. Gentry	Cres.	1	—
D. spathicalyx A. Gentry	Cres.	1	—
Parmentiera cereifera Seem.	Cres.	1	unidentified bats
P. macrophylla Standl.	Cres.	1	—
TOURRETTIEAE			
Tourrettia lappacea (L'Her.) Willd.	cf. Mart. ?	?	not seen

Anemopaegma-type flowers are pollinated mostly by large to medium-sized bees, mostly euglossines and anthophorids. These bees contact anthers and stigma chiefly with the top of the thorax. In addition to their pollinators, these flowers are often visited by nonpollinating nectar and pollen thieves. Small halictid and trigonid bees collect pollen but rarely, if ever, trigger the stigma. Butterflies are frequent visitors but remain entirely outside the tube and contact neither anthers nor stigma; often they only take moisture from the calyx or outside of the corolla. Hummingbirds are regular visitors but puncture the base of the corolla tube just above the calyx with their bills to steal nectar without making contact with anthers or stigma. Xylocopid bees are among the most frequent visitors to *Anemopaegma*-type flowers but are also nectar thieves. They slit the base of the corolla tube with their proboscis to obtain nectar and may slit open every flower of a plant.

The pollination spectrum for *Arrabidaea patellifera*, a typical *Anemopaegma*-type flower observed in Guanacaste, Costa Rica, (8 hours) and the Canal Zone (1 hour) included five species of anthophorids, four species of euglossines (*Eulaema polychroma*, *Euglossa variabilis*, *E. viridissima*, *Euplusia* sp.), all females, a single honey bee (*Apis mellifera*), and an unidentified medium-sized bee perhaps related to the xylocopids. Non-pollinating visitors included *Amazilia* hummingbirds, two species of large *Xylocopa*, small pollen-collecting bees (*Trigona* spp. (2) and a metallic green halictid), numerous butterflies (*Phoebis philea*, *P. sennae*, *Anteos clorinde*, a riodinid, and 6 species of skipper), three vespid wasps, a stratiomyid fly, and an unidentified fly. *Arrabidaea chica* may be chosen as a second example. The pollinator spectrum of a vine of *A. chica* observed in Ecuador (5 hours) was very similar and included euglossines (3 species of *Euglossa*), several genera of anthophorids, along with such non-pollinators as a large xylocopid (*Xylocopa*), small pollen-collecting bees (mostly halictids), vespid wasps, butterflies (hairstreaks and skippers), and hummingbirds (especially *Damophila julie*). (See Table 2 for pollinators of other *Anemopaegma*-type flowers.)

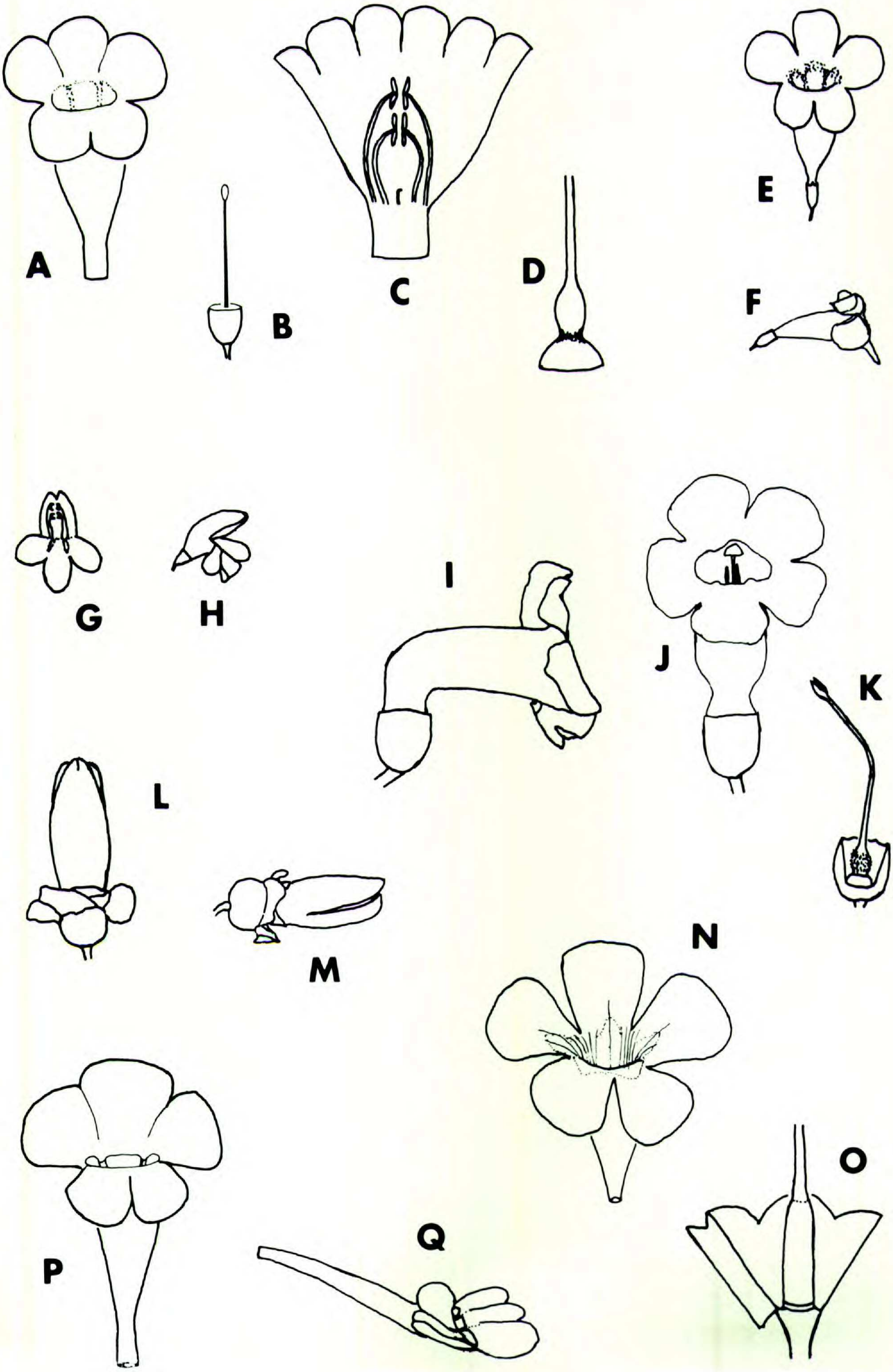
TYNNANTHUS-TYPE.—One of the modifications of the basic pattern is toward smaller, markedly bilabiate corollas with subexserted anthers. I have termed this the *Tynnanthus*-type of morphology (Fig. 3G–H). The corollas of these species are thin-textured and puberulous or lepidote outside. The corolla lobes tend to be almost valvate in bud. The flowers are very fragrant, variously colored, usually have open mouths, and produce nectar. *Tynnanthus*, *Arrabidaea florida*, and *Mussatia* have *Tynnanthus*-type flowers in Central America.

Tynnanthus-type flowers are visited by small bees (halictids and trigonids) and butterflies (mostly skippers). Both types of visitors make contact with the subexserted anthers and stigma and appear to be effective pollinators. The skippers partially enter the corolla tube and contact the anthers with the front edge of their wings or the top of their heads. The pollinator spectrum for a lavender-flowered plant of *Arrabidaea florida* growing on Pipeline Road, Canal Zone (ca. 5 hours of observations) includes two species of halictid, 2 species of trigonid, and 5 species of skippers. A white-flowered plant of the same species growing near the Summit Hills Golf Course, Canal Zone (ca. 6 hours of observation) had a pollinator spectrum including a halictid, 2 species of trigonid, 12 species of skipper, and a hairstreak (lycaenid). An *Epargyreus*-like skipper, several smaller skippers, and some unidentified small bees were observed to visit *Tynnanthus croatianus* near Madden Lake, Canal Zone, (½ hour of observation), and a skipper (*Pholisora* aff. *hayhurstii*) was observed on flowers of *Tynnanthus guatemalensis* in Belize (½ hour of observation). Skippers and small bees were observed at *Mussatia hyacinthina* in Venezuela (½ hour of observation).

PITHECOCTENIUM-TYPE.—An opposite modification of the basic floral morphology results in the *Pithecoctenium*-type flower (Fig. 3I–K). These species have thick, often gland-covered calyces and corollas greatly thickened, especially near the base. The tube is nearly closed near its base by a thickened, densely glandular pubescent ridge at the level of stamen insertion. The corolla tube is rather long, highly puberulous outside, has poorly developed throat ridges, and an open mouth. It is usually bent forward below the middle. The flower is white or cream-colored, has a conspicuous disc, and produces abundant nectar.

→

FIGURE 3. Floral Morphology.—A–F. *Anemopaegma*-type.—A–D. *Anemopaegma orbiculatum*.—A. Corolla in top view.—B. Calyx and pistil (stigma lobes closed).—C. Corolla split open to show stamen placement.—D. Ovary and disc.—E–F. *Arrabidaea candicans*.—E. Flower in top view.—F. Flower in side view.—G–H. *Tynnanthus*-type, *Tynnanthus croatianus*.—G. Flower in front view.—H. Flower in side view.—I–K. *Pithecoctenium*-type, *Pithecoctenium echinatum*.—I. Flower in side view.—J. Flower in bottom view.—K. Pistil, disc, and section through calyx.—L–M. *Amphilophium*-type, *Amphilophium paniculatum*.—L. Flower in top view.—M. Flower in side view.—N–Q. *Cydista* type.—N–O. *Cydista heterophylla*.—N. Corolla in top view.—O. Ovary and part of calyx.—P–Q. *Scobinaria japurensis*.—P. Corolla in top view.—Q. Corolla in side view.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q

Pithecoctenium, *Distictella*, and *Ceratophytum* are Central American genera with this corolla morphology.

Pithecoctenium-type flowers are pollinated by large anthophorids and xylocopids. I have observed an unidentified large bee (*Xylocopa*?) visiting flowers of *Pithecoctenium echinatum* in Belize (½ hour observation) and Paul Opler (personal communication) has recorded numerous visits by *Centris* sp. in Guanacaste, Costa Rica. Flowers with such thick calyces and corollas are apparently immune to nectar robbing by hummingbirds and xylocopids.

Paragonia is of special interest as being halfway between the *Anemopaegma*-type and the *Pithecoctenium*-type. In *Paragonia* the corolla is thicker than in the former but thinner than in the latter. I observed visits by two different species of *Xylocopa* to a *Paragonia pyramidata* vine blooming on the Osa Peninsula of Costa Rica (2 hours of observation, see also Table 2). One species penetrated the corolla base from outside in the usual manner, but the slightly smaller second species entered the flower as a legitimate pollinator. Presumably *Paragonia* represents an intermediate stage in the evolutionary conversion of xylocopid visitors from robbers to pollinators. Additional thickening of the calyx and corolla as in the *Pithecoctenium*-type flower entirely eliminates nectar thieves.

AMPHILOPHIUM-TYPE.—Further modification of the *Pithecoctenium*-type morphology would give rise to the *Amphilophium*-type flower (Fig. 3L–M). In these species the trend toward greater protection of the nectar is carried to such an extreme that the corolla never opens spontaneously and even the pollen is protected inside the flower. The corolla is tubular, extremely thick, and strongly bilabiate with the very thick upper lip formed by fusion of the two upper lobes and the slightly thinner lower lip formed by fusion of the three lower lobes. These two lips remain loosely fused at anthesis unless physically forced apart. In the herbarium the two lips are forced apart by lateral compression of the flower during pressing so that this unique adaptation has gone unremarked. There is a very pronounced ridge at the level of stamen insertion, and the base of the corolla tube below this is convoluted and apparently secretory. The disc is conspicuous and abundant nectar is produced. The calyx is also highly modified and consists of a very thick inner sleeve tightly appressed to the base of the corolla and a thin, loose, uneven, outer rim which is reflexed away from the corolla. The inner surface of the outer calyx and outer surface of the inner calyx are secretory and sticky. Such South American genera as *Glaziovia* have floral morphologies similar to *Amphilophium*.

The *Amphilophium*-type flower is a logical extension of the trend toward greater protection seen in *Paragonia* and *Pithecoctenium*. It has the thickest corolla of all the Central American Bignoniaceae, and its secretory double calyx attracts ants and wasps which presumably give further protection to the flower. The calyx of *A. pannosum* is so viscid that it can protect the flower by trapping small insects. *Amphilophium* pollinators are by necessity large and robust bees including *Megachile* sp., two species of large anthophorid (*Centris*?), and probably xylocopids which physically force the two lips of the unopened corolla apart in order to enter the flower.

CYDISTA-TYPE.—A different modification on the basic *Anemopaegma*-type morphology results in the *Cydista*-type flower (Fig. 3N–Q). In this group the corolla tube is long, dorso-ventrally compressed, relatively funnel-shaped (rather than bell-shaped above a tubular base), and has a wide but narrow mouth. Many species have conspicuous nectar guide lines, these being usually a number of finely pencilled more or less parallel magenta or brick red longitudinal lines converging from the lobes onto the two longitudinal folds in the floor of the corolla tube. Most of these species have the tube glabrous or inconspicuously puberulous outside and relatively thin corollas. Most of the genera included here (*Cydista, Clytostoma, Phryganocydia*) are unusual in lacking a nectariferous disc. The pattern intergrades with the *Anemopaegma*-type from which it is rather arbitrarily separated; for example several species of *Tabebuia* are intermediate between these two morphological types.

The *Cydista*-type flower is, like the *Anemopaegma*-type, pollinated mostly by euglossine bees. However, visitors to most of these species, especially those lacking a nectariferous disc, are very infrequent (see phenology below). I have observed only *Trigona* spp. to visit *Cydista diversifolia*, and these small bees collected pollen without triggering the stigma (5½ hours of observation in Guanacaste, Costa Rica; ½ hour in the Canal Zone). I have seen *Euglossa* spp. (as well as *Trigona* sp.) visit *Phryganocydia corymbosa* in the Canal Zone (ca. 5 hours of observation) and near El Real, Darién Province (ca. 6 hours of observation). I have observed only a single *Exarete*(?) as a potential pollinator of *Cydista aequinoctialis* in ca. 15 hours of observation in the Canal Zone, although small halictids and trigonids visit the flowers. I have observed no visitors to *Cydista heterophylla* (1 hour of observation, mostly in the Canal Zone) and *Clytostoma binatum* (sporadic observation).

Scobinaria is of special interest in being intermediate in several respects between the *Cydista*-type flower and other groups. It is the only genus included here with a conspicuously pubescent corolla tube and the only one which vegetatively has interpetiolar glandular fields. Its corolla is somewhat thicker in texture and more strongly compressed than corollas of other species included here. It is likely that the dorsally compressed corolla of *Scobinaria* (which has a nectariferous disc) was evolved independently from the other *Cydista*-type flowers. Access to the *Scobinaria* flower is more limited than to other *Cydista*-type flowers. In Belize, I observed small non-pollinating halictids and trigonids unsuccessfully attempt to enter the *Scobinaria* corolla, while several larger *Euglossa* spp. forced their way into the corolla tube.

TANAECIUM-TYPE.—The *Tanaecium*-type is one of the most spectacular modifications of bignon floral morphology (Fig. 4A–B). These flowers have a relatively thick and rigid corolla which is white and has a greatly elongated narrow tube. The anthers are subexserted, and the thecae are long and flexuous. They have a conspicuous disc, abundant nectar, a heavy sweet aroma, and open in the evening. This corolla form has evolved separately in the Bigononieae (*Tanaecium*) and the Tecomeae (South American *Tabebuia* spp. and probably *T. striata*).

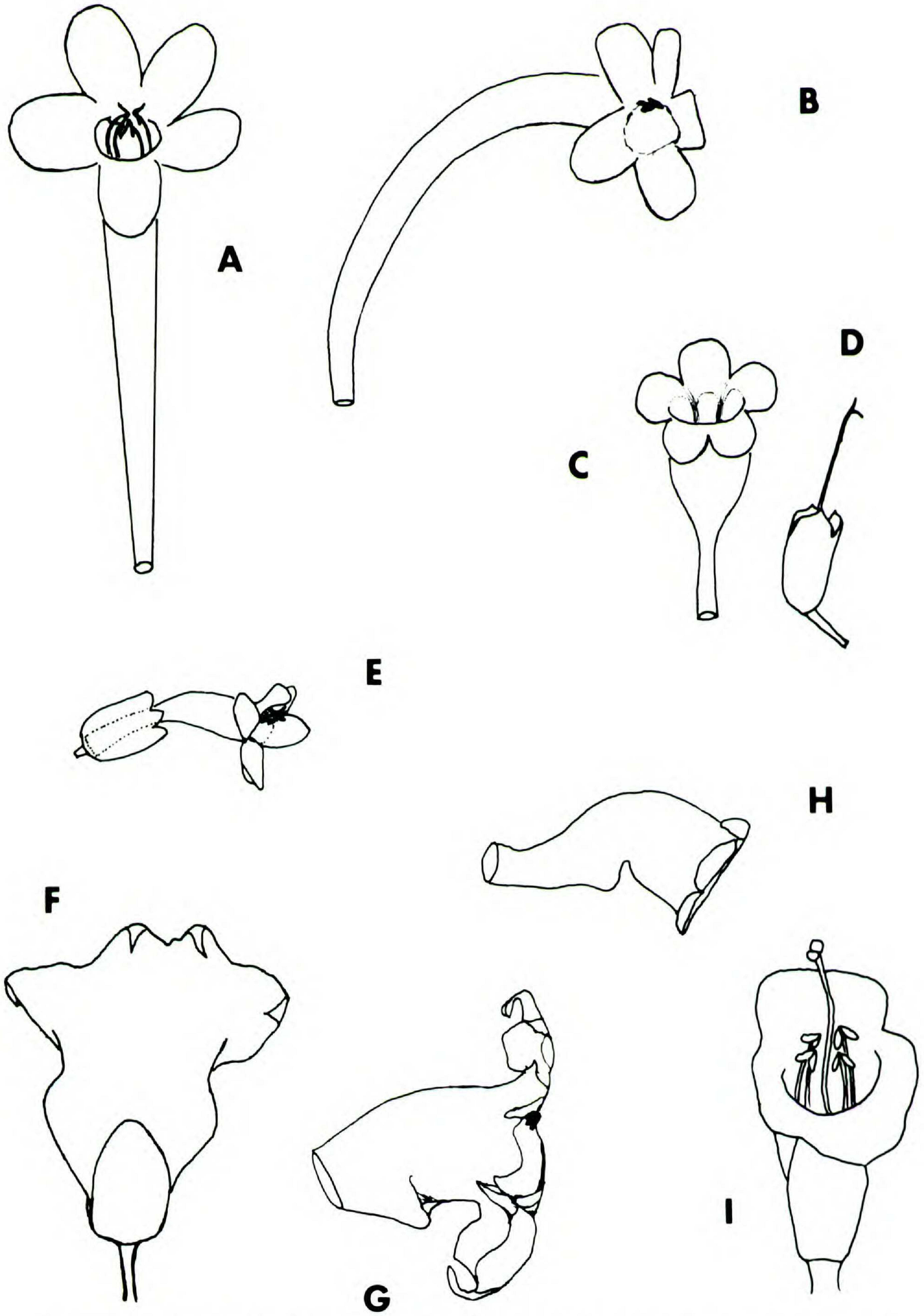


FIGURE 4. Floral Morphology (continued).—A–B. *Tanaecium*-type, *Tanaecium nocturnum*.—A. Corolla in bottom view.—B. Corolla in side view.—C–D. *Martinella*-type.—C–D. *Martinella obovata*.—C. Corolla in top view.—D. Calyx and pistil.—E. *Pachyptera standleyi*, Flower in side view. —F–I. *Crescentia*-type.—F–G. *Crescentia cujete*.—F. Flower in top view.—G. Corolla in side view.—H–I. *Dendrosicus latifolius*.—H. Corolla in side view.—I. Flower in bottom view.

Although I have observed no visitors to *Tanaecium*-type flowers, they fit the classic syndrome for hawk-moth pollination (Faegri & Pijl, 1966). Of all the potential pollen vectors available in Panama, only sphingid moths have long enough tongues to reach the nectar at the bottom of the long (to 17 cm), narrow tube of *Tanaecium.*

MARTINELLA-TYPE.—I have termed another morphological pattern the *Martinella*-type (Fig. 4C–E). These flowers are bright red-orange or deep red-violet (in *Tourrettia* only the calyx is red). The corolla is rather thick in texture, glabrous outside (except *Tourretia*), and has an open mouth, rather long tube, and often exserted or subexserted anthers. It is usually glabrous outside. The two corolla ridges are reduced or accentuated and very close together. The flower is odorless, has a conspicuous disc, and produces abundant nectar. The calyx is usually large and thin and encloses the base of the corolla tube very loosely. These flowers have evolved independently in the Bignonieae (*Martinella, Pyrostegia*) and in the *Tecomeae* (*e.g.* West Indian *Tabebuia* spp. and north temperate *Campsis*).

Martinella-type flowers are pollinated by hummingbirds. In contrast to their usual behavior at other bignon flowers, hummingbirds enter *Martinella*-type flowers from the front. I have observed the little hermit (*Phaethornis languimaris*) pollinate *Martinella obovata* on the Osa Peninsula (ca. 1 hour of observation) and on Santa Rita Ridge (½ hour of observation). This relatively small, short-billed hummingbird sticks its entire head into the campanulately expanded upper part of the tube and contacts the anthers with its forehead and the back of its head. I have also observed larger hummingbirds visit *Martinella*, but even though they approached the corolla from the front their bills were long enough to reach the nectar without contacting the anthers. Trigonids sometimes cut holes in flowers in bud, but I have not seen them visit mature flowers. I observed the approach to a flower of *Martinella* of a single *Euglossa* which left without entering the corolla. Cultivated vines of *Pyrostegia venusta* are often visited by hummingbirds, and its exserted anthers can make contact with both long and short-billed visitors. Red flowers and lack of odor are part of the standard syndrome for bird pollination. Reduction of pubescence probably relates to loss of odor production. The large loosely fitting calyx of several *Martinella*-type species probably serves to discourage puncture of the corolla base in the usual manner. The close-together corolla ridges of *Martinella* apparently act as a guide to direct the pollinator's bill to the basal nectar supply; in other species the more narrowly tubular flower serves this function.

Pachyptera standleyi has an interesting additional modification. Instead of being odorless its flowers have the same unpleasant garlic odor as the vegetative parts of the plant. Presumably this would act as a repellent to odor-sensitive insects but not to birds. I have observed no visitors to *P. standleyi*, but its narrowly tubular red corolla, subexserted anthers, and large inflated calyx are typical of hummingbird-pollinated species.

CRESCENTIA-TYPE.—The final pattern of New World bignon flowers is the *Crescentia*-type (Fig. 4F–I). These species are all members of the Crescentieae (*Crescentia, Parmentiera, Dendrosicus*). The corolla is white or off-white, glabrate, thick in texture, and usually has a transverse fold across the throat, behind which is formed a nectar-storing bulge. It is widely campanulate, with reduced lobes and subexserted anthers and stigma. These flowers have a characteristic musky odor, are more or less cauliflorous, and open at night. They have a very large disc and produce nectar copiously.

Crescentia-type flowers are bat-pollinated. I have observed several species of bats (especially *Glossophaga soricina*) visit *Crescentia alata* and *C. cujete*. The bats contact both anthers and stigma, receiving and carrying large quantities of pollen on the fur of their foreheads. While noctuid moths may also be visitors, they do not seem to make contact with the anthers. Trigonids and hummingbirds may penetrate unopened corollas during the day but are only nectar thieves. Night flowering, extremely copius production of nectar, an open rachitic branching pattern, and cauliflorous flowers are adaptations which clearly facilitate visits by bats.

KIGELIA-TYPE.—One of the additional morphological patterns shown by Old World bignons cultivated in Central America is the *Kigelia*-type. Such plants (*Kigelia* and *Haplophragma* in Panama) have very large, widely campanulate, dull-colored off-white or maroon flowers which are borne outside the canopy either flagelliflorously on long dangling leafless branches (*Kigelia*) or pincushion-style on thick-branched, stiff inflorescences projecting out from the canopy (*Haplophragma*). They have large discs, produce copious nectar, and have the same musky odor as *Crescentia*-type flowers. Like *Crescentia*-type flowers they have reduced corolla lobes, subexserted anthers and stigma, and open in the evening.

The *Kigelia*-type morphology is much like that of the *Crescentia*-type except for the much larger and differently presented flowers. These differences are related to evolution for pollination by Old World Megachiropteran bats (Harris & Baker, 1958; Pijl, 1956). Megachiropteran bats are generally larger than the Microchiropteran, New World, flower visiting bats and have a more poorly developed sonar system for navigation (Faegri & Pijl, 1966). These features correlate with larger flowers presented entirely outside the canopy as in the *Kigelia*-type of bignon. In cultivation in the New World these plants are rarely pollinated, although avidly visited by bats. Apparently their visitors are too small to make effective contact with anthers and stigma.

SPATHODEA-TYPE.—The second peculiarly Old World morphology is the *Spathodea*-type. Flowers of *Spathodea* are bright red, usually with a yellow border, glabrous, very large, widely campanulate, medium-textured, and have subexserted, flexuous anthers. The anthers and stigma are held loosely against the inner side of the corolla. The calyx is large and spathaceous. The flower has very little odor, a large disc, and produces abundant nectar.

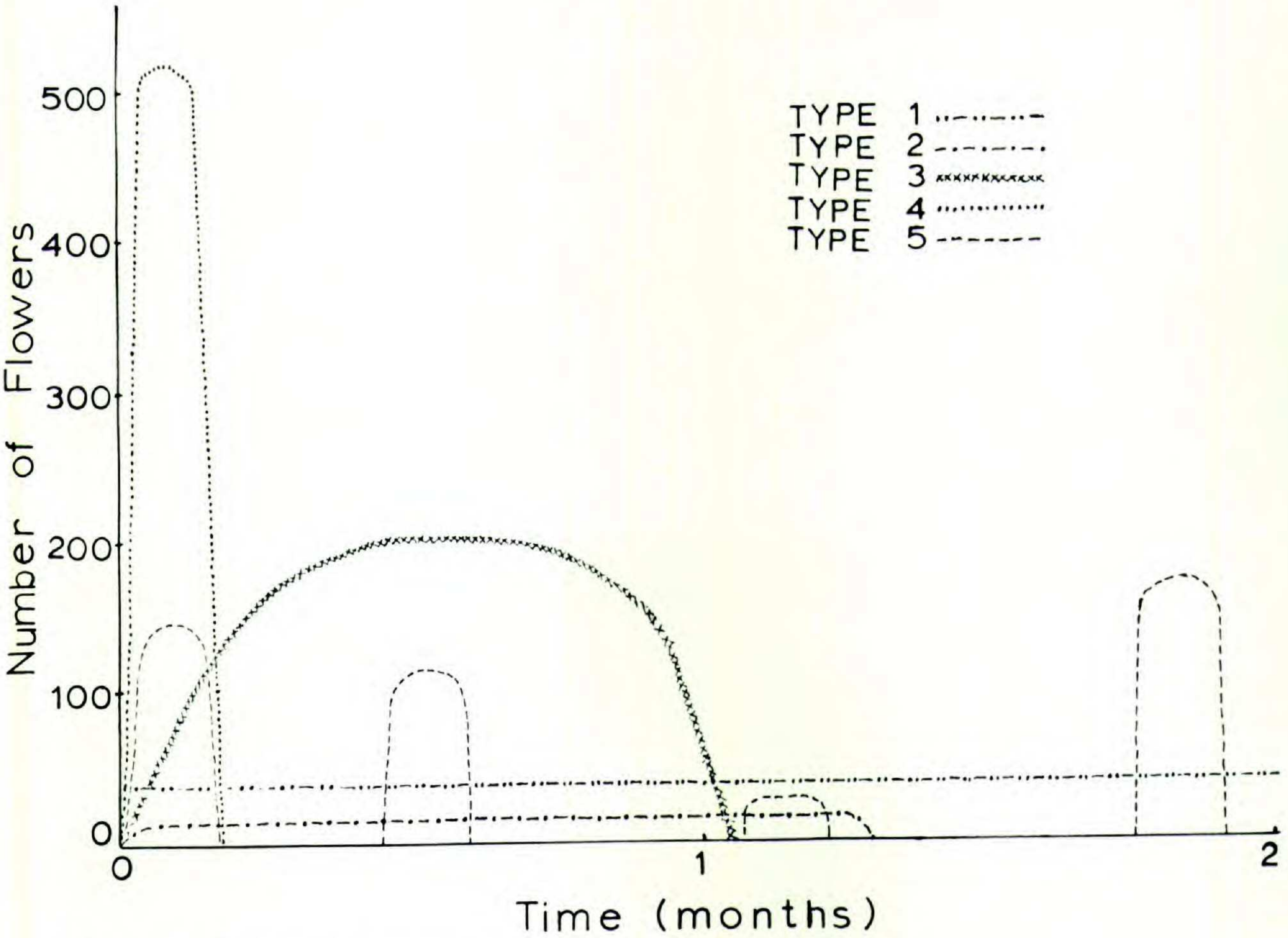


FIGURE 5. Schematic summary of phenology types.

The *Spathodea*-type flower is bird pollinated and is similar to hummingbird-pollinated New World species in such traits as red color, lack of fragrance, production of copious nectar, and subexserted anthers. However, it differs conspicuously in its open, bowl-shaped form and the position of its stamens. These differences correlate with lack of hummingbirds in the Old World and pollination by nonhovering birds (Faegri & Pijl, 1966). The reflexed spathaceous calyx makes a convenient perch from which non-hovering birds can reach the nectar inside the corolla tube.

PHENOLOGY

Different genera and species of Bignoniaceae exhibit strikingly different patterns of flowering phenology. These are related to different strategies of effecting pollination and can be broadly categorized into five major flowering types (Fig. 5, Table 3). Both Types 1 and 2 correspond to Janzen's (1971) trapline syndrome. I have tentatively separated them on the basis of different patterns of duration of flowering and different numbers of flowers produced. Type 4 and some species of Type 3 fall into the mass flowering syndrome as elucidated by Janzen (1967*a*; personal communication cited in Frankie *et al.*, 1973). Mass flowering has been subjectively defined and based mostly on general appearance of the flowering plant. In general, Type 3 species of Bignoniaceae (*e.g. Tabebuia rosea, Jacaranda caucana* subsp. *sandwithiana*, Fig. 8E) which bloom while deciduous would be classed as mass flowerers by many

TABLE 3. Summary of phenological types.

	1	2	3	4	5
Unit of attraction	single flower	single flower	mass of flowers and buds	mass of flowers	mass of flowers
Duration of flowering cycle	all year	3–8 weeks	3–10 weeks	few days	few days
Seasonality	little or none	little or none	strong: wet or dry season	dry season only	little or none
Flower presentation	single cauliflorous flowers	few flowered axillary inflorescence	large many flowered inflorescence	term. many flowered inflorescence	clustered axillary inflorescence
Anthesis	evening	very early morning	morning: after daybreak	mostly morning	very early morning
Duration of one flower	1 night	(1–)2 days	1 day	2 days	2–3 days
Synchronization with adjacent plants	none	little or none	only as to seasonality	near perfect	very strong
Number of flowering cycles in a year	one	probably one or two	one	either one or two	many
Number of flowers produced at a time at maturity	few to 40	mostly less than 10	many (to few thousand)	many (to 10,000) canopy	few to many (variable)
Location of inflorescence	low; often near ground	below canopy; mostly pendent	mostly in canopy	(leaves usually deciduous)	on young branchlets; low or high
Nectar production	copious	some	some	some	usually none

authors. Mass flowerers may bloom for a few days or several weeks and thus have very different patterns of flower production. While general appearance is perhaps more important than duration of flowering in terms of pollinator attraction, length of flowering and number of flowers produced are more important to the plant in terms of energy expenditure (*cf.* Heinrich & Raven, 1972). Because of this difference in viewpoint, I have used the term "cornucopia" species for Type 3 bignon and the term "big bang" species to refer to bignons with a Type 4 phenology. Most of my observations of phenological patterns were made in Panama, and a list of Panamanian species noting phenological type and observed pollinators is included in Table 2.

The Type 1 ("steady state") flowering pattern (Fig. 6) is correlated with *Crescentia*-type flowers and pollination by bats. The key feature of this phenological type is production of flowers almost every day throughout the reproductive life of a plant. Type 2 ("modified steady state") species (Fig. 7) are bee-pollinated. They differ from Type 1 species chiefly in shorter flowering periods.

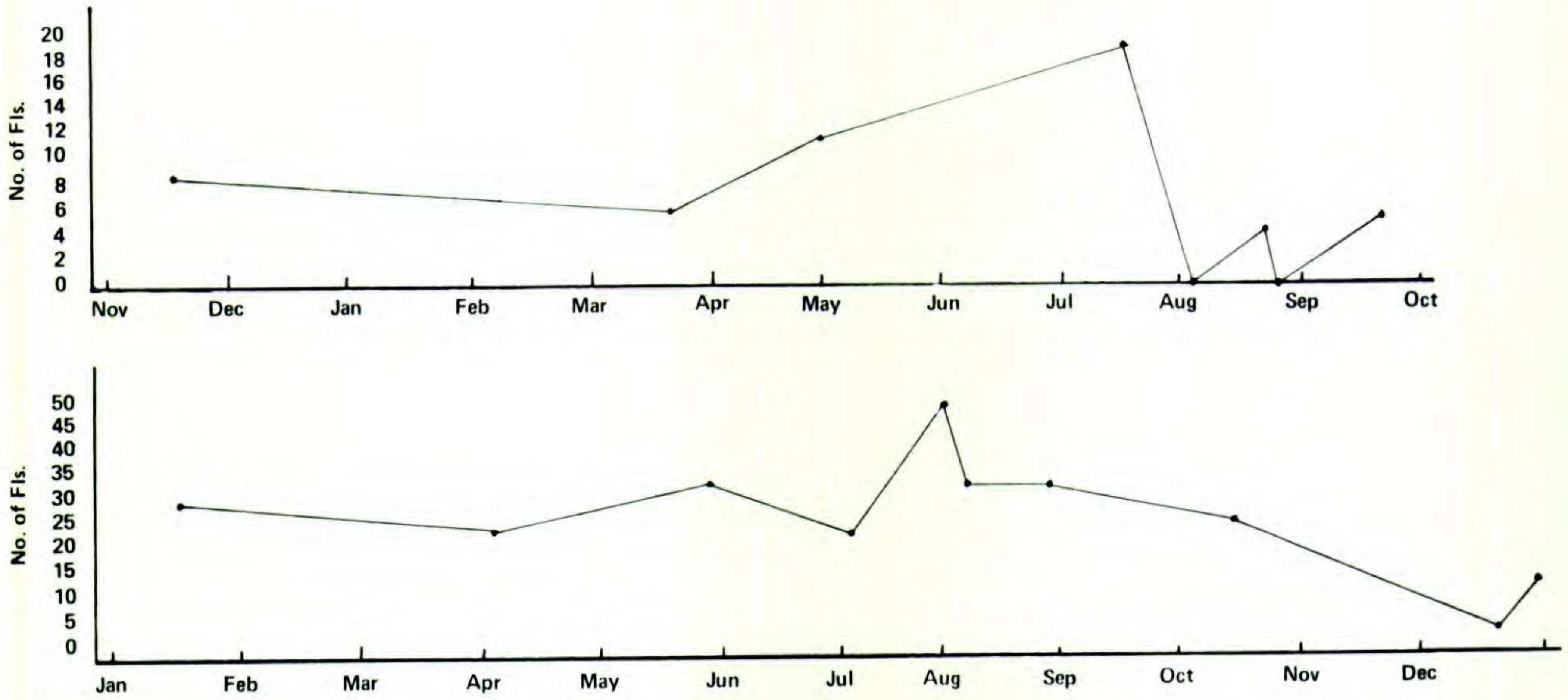


FIGURE 6. Examples of Type 1 ("steady state") phenology. Top. *Parmentiera cereifera* tree at end of "Boy Scout Camp Road" near Madden Lake, Canal Zone. Bottom. *Crescentia cujete* tree in Los Ríos, Canal Zone.

However flowering may be interrupted in some individuals of a Type 1 species, in which case this flowering pattern approaches that of Type 2. Another difference between bat-pollinated "steady state" species and the bee-pollinated species of Type 2 is in the larger numbers of flowers usually produced each day (or night) by the former. Of course diurnal differences in time of anthesis are also present between the two types. Although separation of Type 1 and Type 2 species is not clear cut in every instance, the flower production patterns of representative individuals of the two groups which I followed closely appear sufficiently different to merit their distinction.

Both "steady state" phenologies are associated with pollination by long-lived pollinators which establish fixed daily foraging routes (termed trapliners by Janzen, 1971). In comparison with other phenological types, "steady state" species open very few flowers at a time and bloom for a longer period. There is little seasonality or external synchronization of flowering and individual plants of "modified steady state" species are dependent on chance overlap of flowering periods to provide opportunity for cross-pollination.

Both of the strictly mangrove species of Bignoniaceae in Panama and Costa Rica (*Phryganocydia phellosperma* and *Tabebuia palustris*) have a modified form of Type 2 phenology. Plants of these species produce only one or two flowers at a time at sporadic intervals. Since these species grow in relatively dense stands, the population as a whole presumably fulfills the role of continual pollinator attraction.

The Type 3 or "cornucopia" phenology (Fig. 8) is the generalized Bignoniaceae flowering strategy and is shown by most temperate plants (Gentry, 1974). All hummingbird, hawkmoth, and bee/butterfly pollinated Panamanian and Costa Rican species have this phenology as do many bee-pollinated species. Type 3 species bloom for from a few weeks to over a month. The flowers usually last a single day. Flowering is seasonal, but flowering of individual plants of

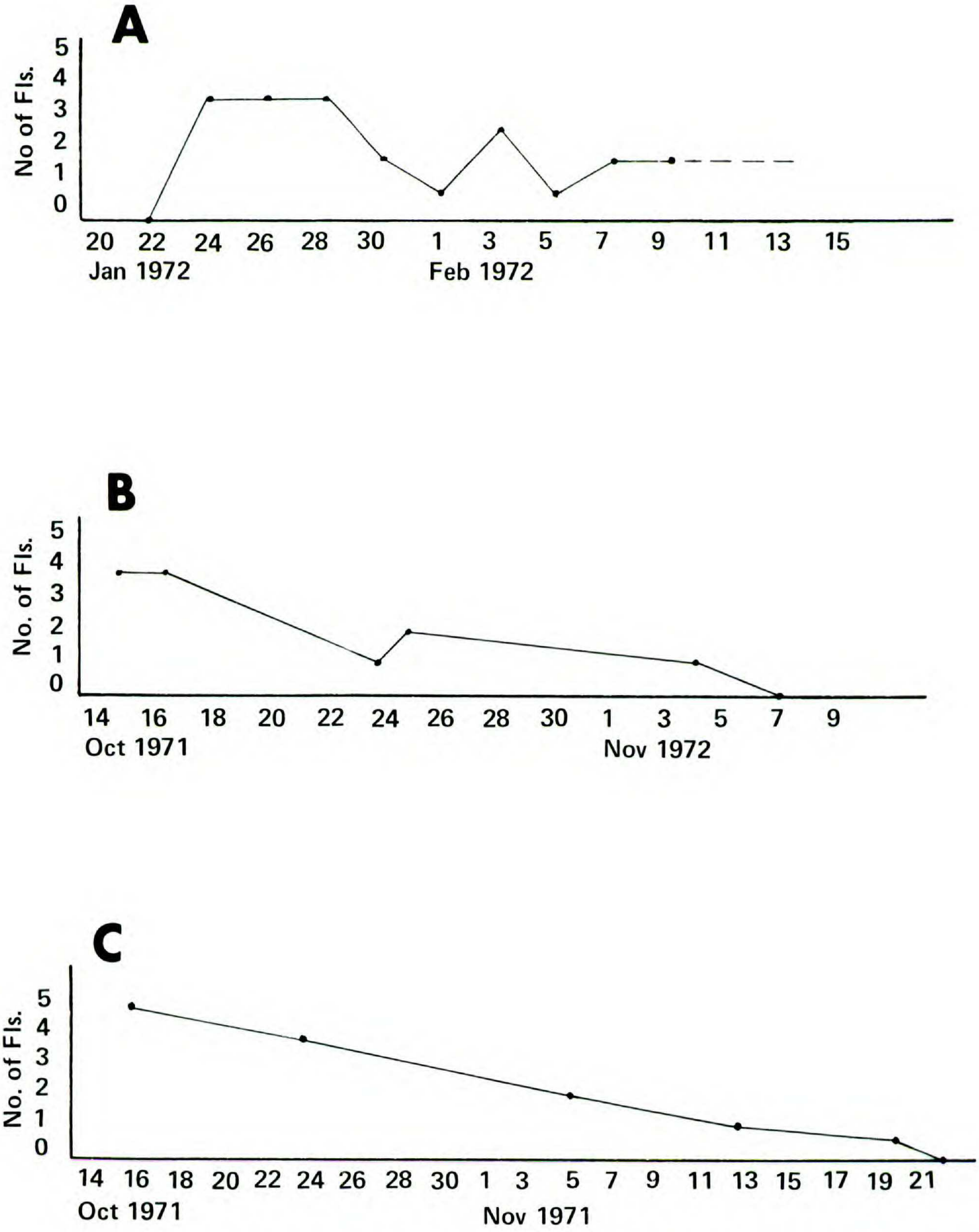


Figure 7. Examples of Type 2 ("modified steady state") phenology.—A. *Anemopaegma chrysoleucum* vine at junction of Ríos Espavé and Bayano, between Cañitas and Agua Clara; predicted from size classes of buds on first day of flowering, 26 Jan. 1972.—B. *Stizophyllum riparium* vine on Pipeline Road, Canal Zone; first observed in October 1971, but presence of mature fruit at that time indicates a flowering period beginning in September.—C. *Amphilophium paniculatum* vine at entrance to Pipeline Road, Canal Zone.

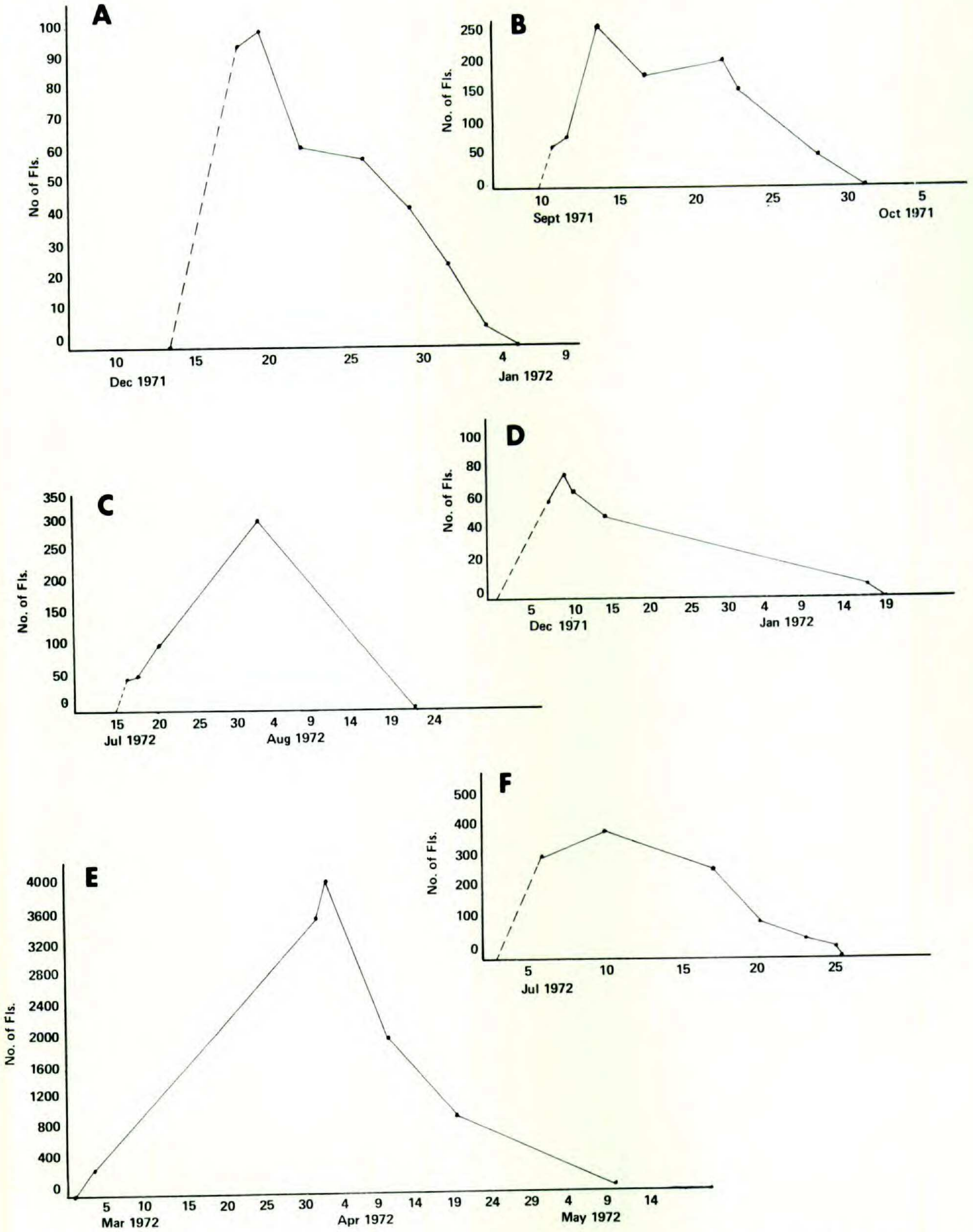


FIGURE 8. Examples of Type 3 ("cornucopia") phenology.—A. *Arrabidaea candicans* vine near Number 23, Pipeline Road, Canal Zone; the plant was rather immature with only a single flowering branch.—B. *Arrabidaea florida* vine on Pipeline Road, Canal Zone.—C. *Tynnanthus croatianus* vine on "Boy Scout Camp Road," Canal Zone.—D. *Tecoma stans* shrub at base of Sosa Hill, Canal Zone.—E. *Jacaranda caucana* subsp. *sandwithiana* tree cultivated at Summit Garden, Canal Zone.—F. *Arrabidaea patellifera* vine near Paraiso, Canal Zone.

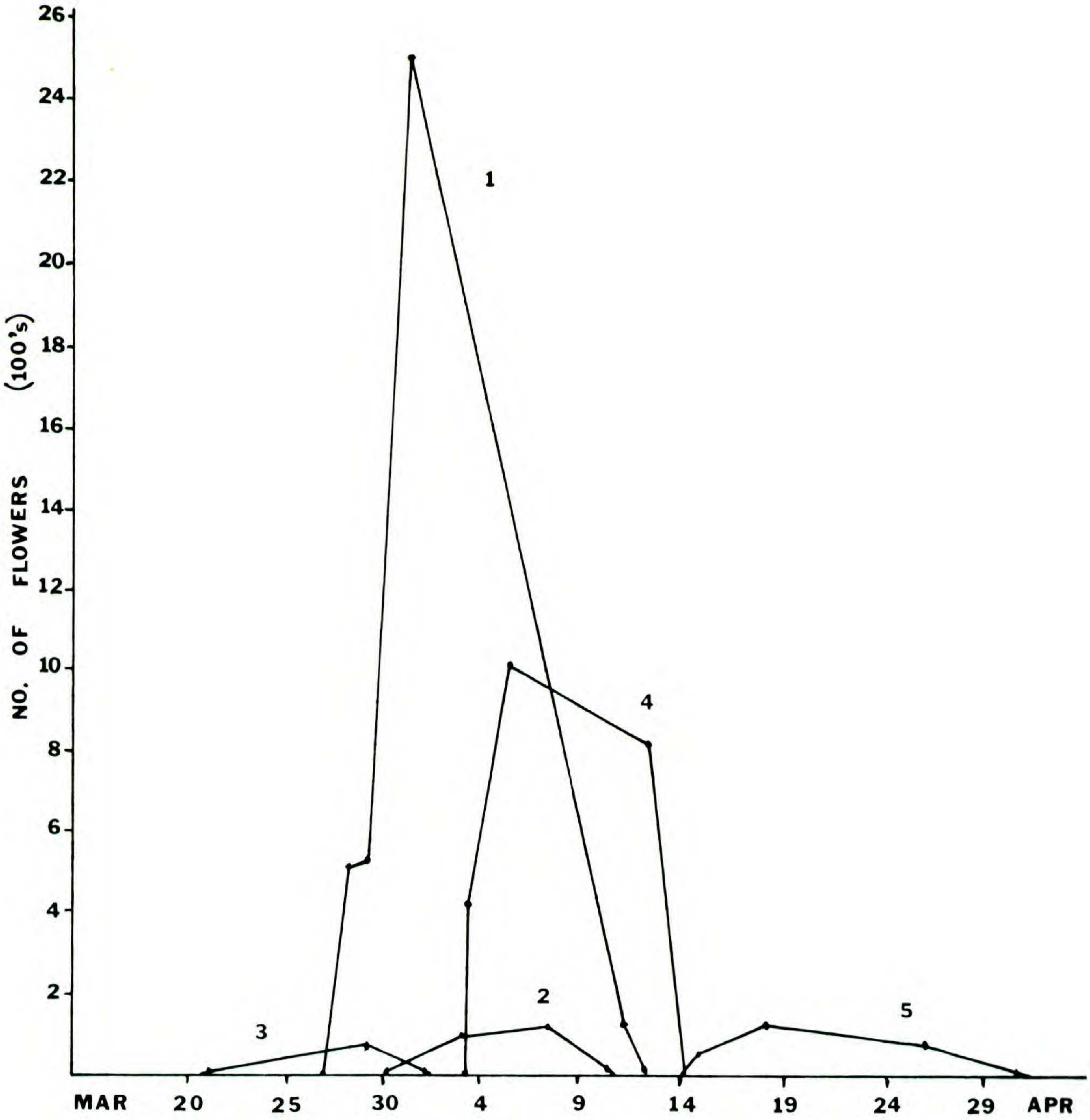


FIGURE 9. Phenology of several vines of Type 3 *Xylophragma seemannianum* illustrating overlap of flowering periods without synchronization. Vine 1—near beginning of pavement on Pipeline Road, Canal Zone; Vine 2—0.5 miles N of first gate on Pipeline Road, Canal Zone; Vine 4—near Paraiso, Canal Zone; Vine 5—near Summit Garden, Canal Zone.

a species is synchronized only as to season (Fig. 9). Dry season bloomers of Type 3 (Fig. 8A, D, E; Fig. 9) often flower while deciduous and appear to be "mass flowerers," while species flowering with their leaves can produce the same number of flowers over the same time span without appearing to be mass flowerers. *Paragonia pyramidata* is exceptional in having Type 3 flower production but lacking seasonality; perhaps it is significant that fruit set is less frequent for *Paragonia* than for most other Type 3 species.

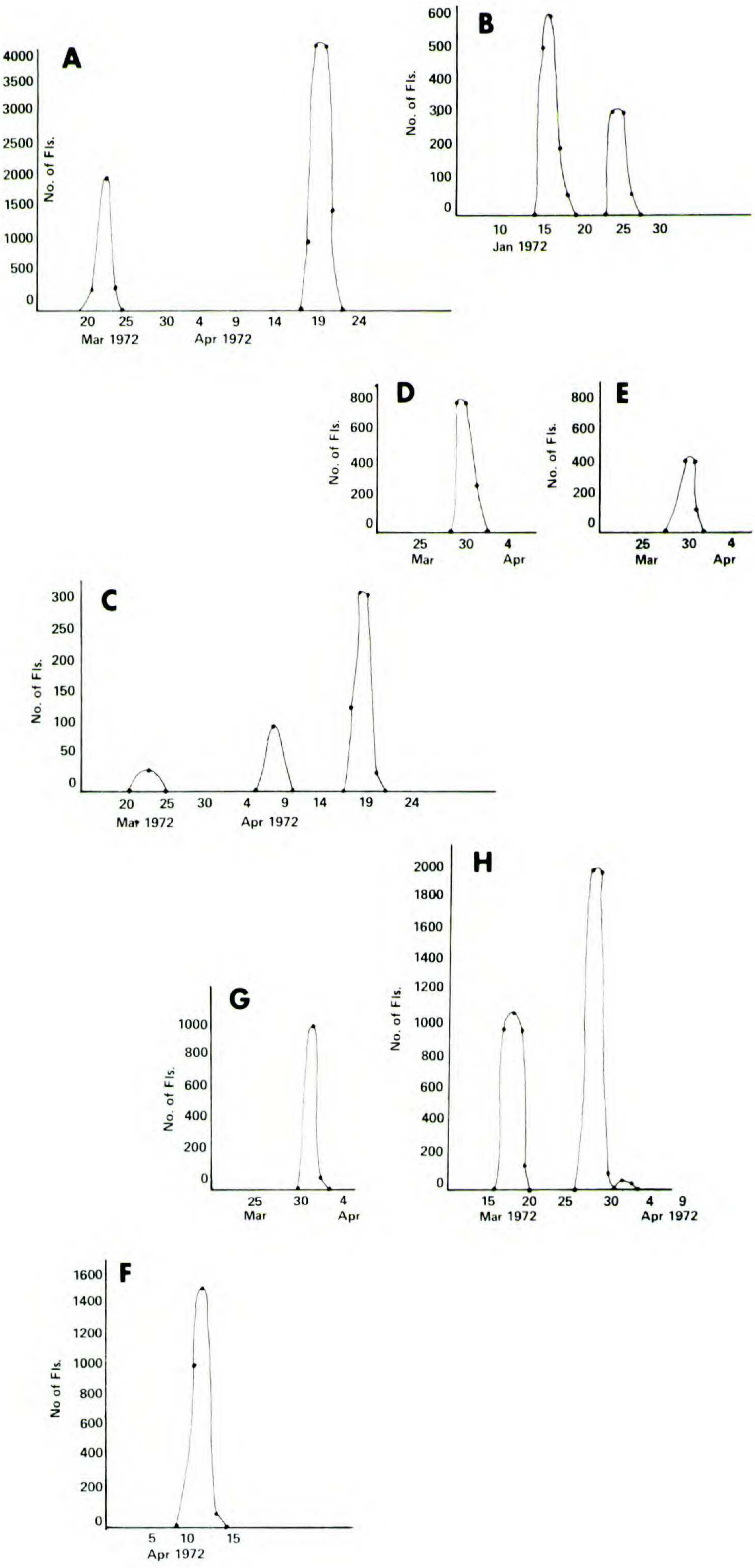
The Type 4 ("big bang") flowering type (Fig. 10) is characterized by a single brief highly conspicuous burst of mass flowering with the production of a great many flowers, each lasting about two days. All "big bang" species flower during the dry season. Blooming is highly synchronized between different individuals so that most of the plants of a species in a community bloom at the same time. Each flowering cycle is only a few days in duration. These plants seem to attract a generalized spectrum of pollinators, mostly bees, and appear to be an important source of both nectar and moisture for the insect members of a community during their brief burst of flowers.

Tabebuia guayacan epitomizes this phenological pattern with up to an estimated 10,000 flowers covering a single tree for four short days. Many observed trees of *T. guayacan* showed flowering curves as in Figure 10D–E; others bloomed twice during the dry season (Fig. 10A–B). One tree actually bloomed three times (Fig. 10C), but one of these blooming periods involved only a single lower branch. Trees of *Tabebuia ochracea* subsp. *neochrysantha* showed the similar pattern illustrated in Figure 10H. Vines of *Macfadyena unguis-cati* bloomed with the pattern shown in Figure 10F–G.

It is noteworthy that all of these plants are dry season bloomers (see Janzen, 1967, for additional discussion). It seems quite possible that only in the dry season can a tree or vine attract potential pollinators from a sufficient distance to achieve high pollinator density and hence good fruit set during such a short period of flowering. During the wet season potential pollinators presumably are under less stress and can utilize alternate, more long-lasting and dependable resources for nectar or moisture. Even though occasional individuals of the species utilizing the "big bang" flowering strategy do flower during the wet season, I have never observed these wet-season flowerings to produce fruit, although sometimes several plants will bloom together so that cross-pollination should be possible. It is also probable that synchronization of flowering between different trees, apparently related to water stress, is more precise during the dry season.

Plants of flowering Type 4 show an amazing coordination of flowering periods between the different individuals of a population. *Tabebuia guayacan* (Fig. 11), for example, synchronizes its flowering so that virtually all of the trees in an area bloom during the same few days of the year. *Tabebuia ochracea* subsp. *neochrysantha* shows the same phenomenon, as does *Macfadyena unguis-cati* to a lesser extent. This exact synchronization contrasts sharply with the relative asynchrony of a typical Type 3 flowerer like *Xylophragma seemannianum* (Fig. 9) (see also Croat, 1969).

Type 5 or "multiple bang" flowering (Fig. 12) appears to be the most specialized of all in many respects. The plants in this group, all vines, have numerous short flowering periods (ca. 3 days) scattered throughout the year. Each individual flower lasts two or three days. Synchronization between different individuals of a population is extremely good. For example, on 21 December 1971 a very noticeable percentage of the trees in the Canal Zone were covered with the purple flowers of vines of *Phryganocydia corymbosa* whereas on 20 December and 23 December not a single flowering *Phryganocydia* was evident. Flowering is usually not so conspicuous, however, and a plant often produces only a few flowers during a given flowering cycle. In addition to intraspecific synchronization of flowering periods, there is a marked tendency for all the


A
No. of Fls.
4000
3500
3000
2500
2000
1500
1000
500
0
20 25 30 4 9 14 19 24
Mar 1972
Apr 1972
B
No. of Fls.
600
500
400
300
200
100
0
10 15 20 25 30
Jan 1972
D
No. of Fls.
800
600
400
200
0
25 30 4
Mar Apr
E
No. of Fls.
800
600
400
200
0
25 30 4
Mar Apr
C
No. of Fls.
300
250
200
150
100
50
0
20 25 30 4 9 14 19 24
Mar 1972
Apr 1972
H
No. of Fls.
2000
1800
1600
1400
1200
1000
800
600
400
200
0
15 20 25 30 4 9
Mar 1972
Apr 1972
G
No. of Fls.
1000
800
600
400
200
0
25 30 4
Mar Apr
F
No of Fls.
1600
1400
1200
1000
800
600
400
200
0
5 10 15
Apr 1972

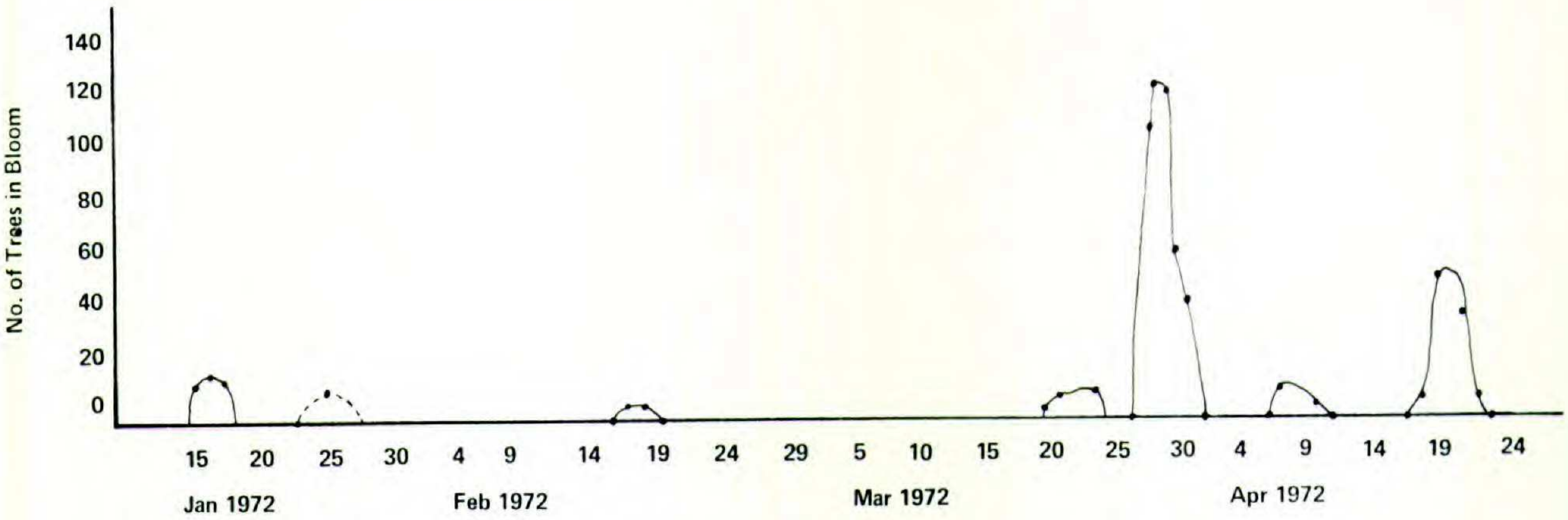


FIGURE 11. Synchronization of flowering in *Tabebuia guayacan*.

species exhibiting this flowering strategy to bloom at the same time (Fig. 12). There is a general lack of synchronization of different branches of the same plant, although each branch may bloom synchronously with other plants of the population.

I think that this type of reproductive behavior is triggered by vigorous vegetative growth so that all plants in an area may achieve synchronization through similar response to optimal growth conditions, *e.g.* a good rain. That moisture or possibly an associated temperature phenomenon (see Schulz, 1940) triggers flowering in plants of this group is indicated by some circumstantial evidence. For example, during the wet season and early dry season a *Cydista aequinoctialis* vine growing at Summit Gardens flowered once every few weeks in synchrony with other plants of the species in the vicinity (Fig. 12A–C), but with onset of the dry season it was subject to regular irrigation and during February and March bloomed almost every day in contrast to non-irrigated vines which bloomed hardly at all during this period.

One of the most interesting aspects of many "multiple bang" species is their lack of a nectariferous disc and apparently of nectar production as well. As might be expected, these species receive very few visits from prospective pollinators, and all such visits are very brief, being confined to penetration of only one or two flowers. Although small pollen-collecting bees do visit these flowers, their activity does not trigger the stigma so their value as pollinators seems to be nil. I interpret these species (*Cydista aequinoctialis*, *C. diversifolia*, *C. heterophylla*, *Phryganocydia corymbosa*, and *Clytostoma binatum*) as mimics of nectar-producing mass flowering species, including other Bignoniaceae, which are dependent for pollination on exploratory visits by nectar-seeking bees in-

---

←

FIGURE 10. Examples of Type 4 ("big bang") phenology.—A. *Tabebuia guayacan* tree near Summit Gardens, Canal Zone.—B. *Tabebuia guayacan* tree cultivated at Summit Gardens, Canal Zone.—C. *Tabebuia gauyacan* tree at Madden Wye, Canal Zone.—D. *Tabebuia guayacan* tree near Gamboa airport, Canal Zone.—E. *Tabebuia guayacan* tree near grease pit just outside Gamboa, Canal Zone.—F. *Macfadyena unguis-cati* vine near Madden Dam, Canal Zone.—G. *Macfadyena unguis-cati* vine near Pedro Miguel, Canal Zone.—H. *Tabebuia ochracea* subsp. *neochrysantha* tree near Miraflores Lake, Canal Zone.

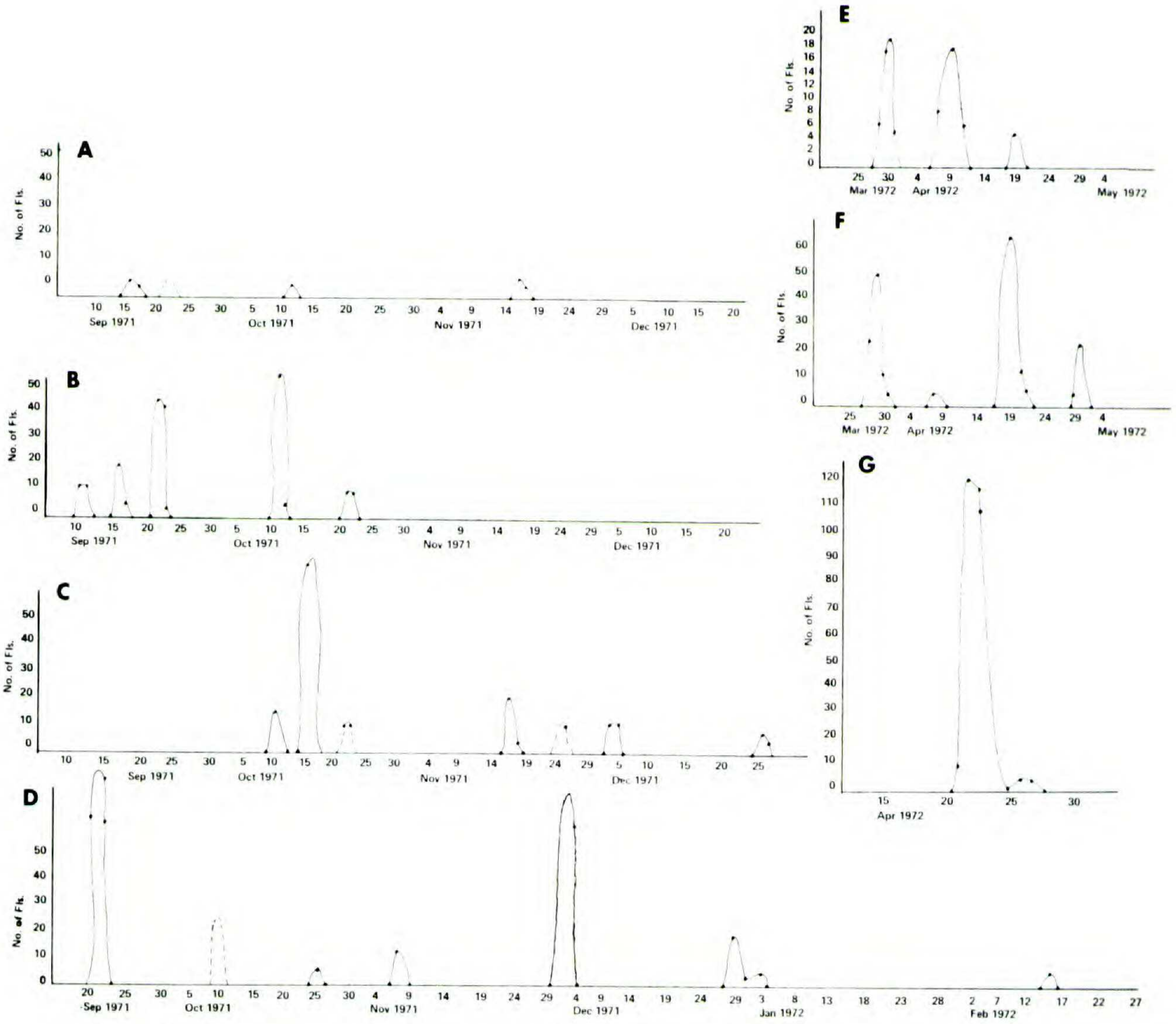


FIGURE 12. Examples of Type 5 ("multiple bang") phenology.—A. *Cydista aequinoctialis* vine at Summit Herbarium, Canal Zone.—B–C. *Cydista aequinoctialis* vines across highway from Summit Hills Golf Course.—D. *Phryganocydia corymbosa* vine near Number 23, Pipeline Road, Canal Zone.—E. *Anemopaegma orbiculatum* vine near Number 23, Pipeline Road, Canal Zone.—F. *Anemopaegma orbiculatum* vine just inside first gate on Pipeline Road, Canal Zone.—G. *Cydista heterophylla* vine near Summit Garden, Canal Zone.

vestigating apparent new nectar sources. Repeated but separated short bursts of flowering allow maximum exposure to naïve prospective pollinators of new flowers to be investigated; few flowers are wasted on bees which have already learned that they are unsuitable nectar sources. Conspicuous visual and olfactory stimuli aid in attracting first-time visitors. Physiologically the plant saves the energy it would have expended on nectar production, and it also avoids the destructive visits of such nectar-thieves as xylocopid bees and hummingbirds. In addition, the lack of repeated visits by foraging bees to flowers on the same plant assures a very high degree of cross-pollination should pollination be effected at all. That this reproductive strategy is eminently successful is evidenced by a tremendous abundance of young post-seedling plants and also the relative commoness of mature vines; *Phryganocydia corymbosa* and *Cydista aequinoctialis* are the two commonest species of Bignoniaceae in the Canal Zone. In fact it is possible that this strategy could only be successful in a very common species where there is a relatively high chance that a randomly foraging prospective pollinator will encounter two plants of the same species more or less in succession.

Not all of the plants with "multiple bang" flowering phenology are non-nectar producing mimics. *Anemopaegma orbiculatum* (Fig. 12E–F), for example, illustrates this flowering pattern while maintaining nectar production. It is subject to extensive corolla damage from nectar-robbing xylocopid bees and sets no more fruit than the species without nectar. Conceivably this is an intermediate step in development of the mimicking phenomenon.

Another variant is *Cydista heterophylla* (Fig. 12G) which apparently has only one or two flowering periods in a year and blooms only in the dry season. I have never actually seen a vine of this species undergo more than a single flowering period, but the occasional occurrence of fruit on a flowering vine indicates at least two such periods for some individuals. The flowering strategy of this species is perhaps closer to Type 4 than Type 5, although it is more closely related to the "multiple bang" flowerers.

DISCUSSION OF PHENOLOGY

These five major flowering phenologies correlate rather well with a whole syndrome of reproductive behavior as summarized in Table 3.

Intuitively the basic phenological pattern should be Type 3, in which a plant has a definite, prolonged, flowering season, blooming profusely and continually for a number of weeks. Although containing a number of heterogeneous elements, this phenological type is probably natural in the sense that it encompasses the putative ancestral pattern of the family. The type 3 pattern serves as a convenient base line for discussion of the other flowering types.

Selection for conservation of reproductive energy (*cf.* Heinrich & Raven, 1972) would favor production of few flowers, given adequate pollination of the consequently less attractive flowering plant. By utilizing the constant behavioral patterns of many of the larger long-lived tropical bees (Janzen, 1971), the plants of flowering Type 2 have been able to afford a dramatic reduction in the amount of energy expended on flower production. Further modifications are the tendency to prolongation of flowering and the elimination of seasonality. Both modifications provide a more constant nectar source through time for the pollinator and hence favor its increased utilization of this resource making it in turn a more reliable pollen vector. Many "modified steady state" species have high local population densities as along rivers or in swamps. Such a distribution of individual plants would make cross pollination more frequent.

The mass flowering strategy of species with Type 4 phenology makes possible a different utilization of the same group of pollinators. It depends upon attracting large numbers of bees by disruption of established behavior patterns. Given a suitable environmental trigger, through which individual plants of a species can coordinate flower production, it becomes energetically advantageous for such opportunistically pollinated plants to have shorter more synchronized flowering periods concentrating reproductive energy into a single burst of flowering. Even though it produced many fewer flowers than a species with Type 3 phenology, such a plant could be much more conspicuous during its short flowering period and divert many of the potential pollinators of an area to its munificient supply of nectar. This is exactly what happens with such species as *Tabebuia impetiginosa* and *T. ochracea* subsp. *neochrysantha*, where dozens or even hundreds of pollinators concentrate on these trees during their few short days of flowering. This phenomenon is certainly augmented by dry season flowering when general moisture shortage should force maximum utilization of a large new nectar supply, and the loss of leaves by many trees makes flowering plants more conspicuous and visible for greater distances (see also Janzen, 1967*a*).

Many Type 4 individuals have two flowering periods separated by a few weeks; in both of these they are coordinated with many other plants of the same species. I have actually observed one tree of *Tabebuia guayacan* to flower three times during one dry season, although during the first flowering period only a single branch was in bloom. It is quite possible that from such a phenomenon could be developed the Type 5 phenology wherein many plants of a species bloom synchronously for short periods which are less spectacular and scattered throughout the year. A more measured response to the same or a similar stimulus as that producing the Type 4 flowering burst could easily have led to the Type 5 phenology.

Alternately Type 5 phenology could be a modification of the Type 2 pattern. This idea is supported by the lesser flower production of Type 5 than of Type 4 plants, their lack of seasonality, and by the Type 5 phenology of a species of *Anemopaegma* (*A. orbiculatum*) while other species of the genus show Type 2 flowering. Under this hypothesis, development of a flowering response to some environmental trigger, probably related to rainfall, could give short synchronized flowering periods often with production of relatively few flowers at one time.

In either case, the significance of Type 5 phenology is in making possible yet another utilization of the same limited group of bee pollinators. The Type 5 species rely on the same mass attraction as the Type 4 species but by multiple flowering periods avoid putting all their eggs in one basket as do the Type 4 flowers. Very short flowering periods insure that a significant percentage of visits to Type 5 plants are by bees investigating the flowers as potential nectar sources for the first time. Hence loss of nectar production and reliance on mimicry of nectar-producing flowers becomes a reasonably effective as well as energetically advantageous pollination strategy. These species can thus make use of the same bees which pollinate species with "steady state" or "cornucopia" strategies, since the occasional investigative visits which suffice to pollinate these non-nectar producers interfere very little with established visitation patterns.

SEASONALITY

Seasonality of flowering is, of course, a well-known isolating mechanism making possible greater intracommunity diversity. In the Bignoniaceae it is important only to "cornucopia" and "big bang" species. Although the "big bang"

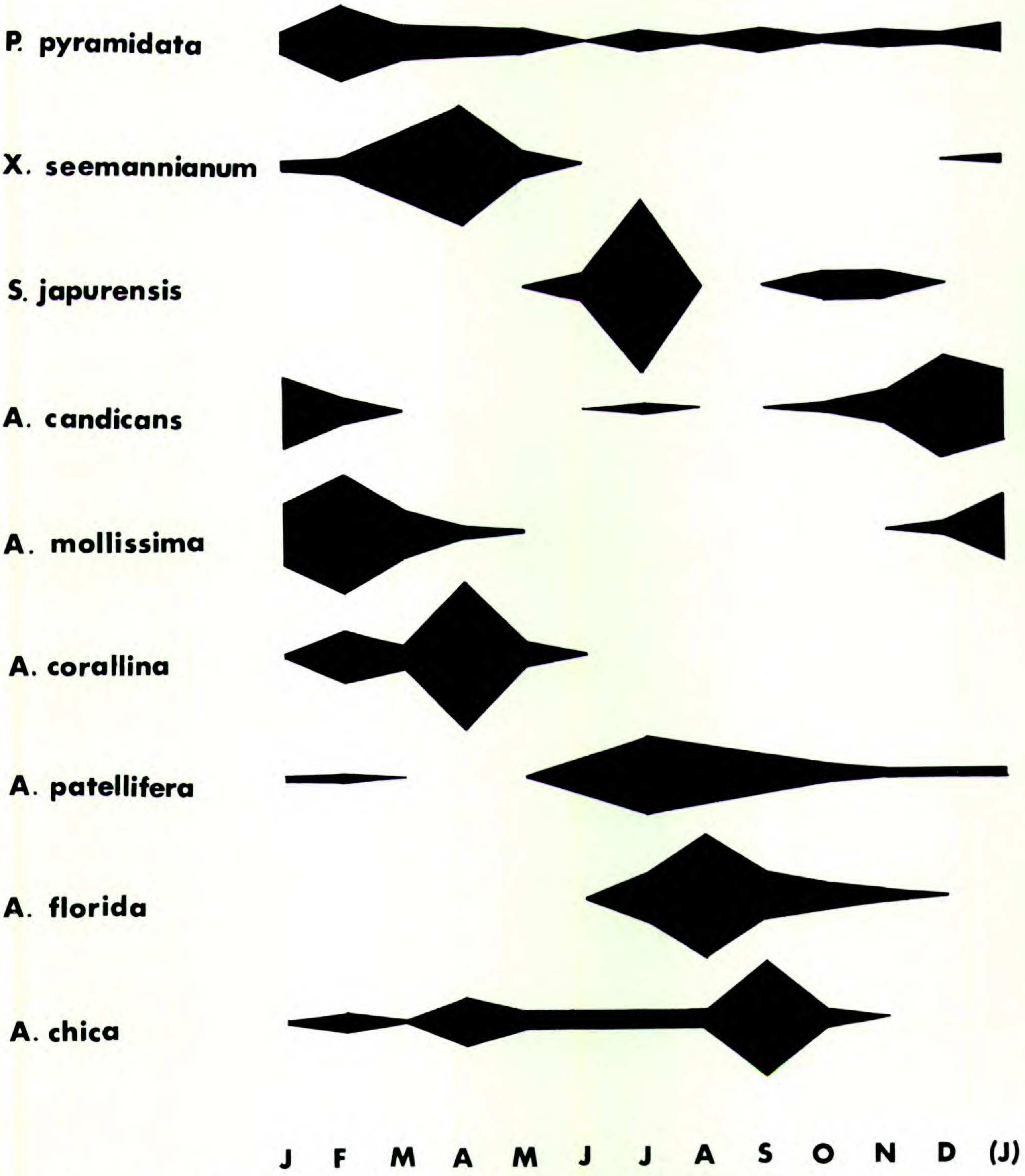


FIGURE 13. Seasonal distribution of commoner Type 3 nectar sources.

phenology implies a kind of seasonality in its restriction to the dry season, seasonality as a means of increasing diversity is only apparent in "cornucopia" species. The various species of *Arrabidaea* are the best examples with *A. candicans* flowering in early and mid dry season, *A. corallina* and *A. mollissima* in mid dry season, *A. patellifera* in early wet season, *A. chica* in early to mid wet season, *A. pubescens* in mid wet season, and *A. florida* in mid to late wet season in Panama. Each species of *Arrabidaea* has its flowering peak in a different month (see Gentry, 1974). As a whole such species, especially when taken in conjunction with Type 4 "big bang" species, provide an important and almost year round source of nectar for the pollinators of a community (Fig. 13).

SUMMARY

While interactions with herbivores and frugivores have been important in bignon evolution, pollinator interactions provide the most spectacular coevolutionary examples. I have attempted to make three points about coevolution between bignons and their pollinators.

1. The family has radiated in floral morphology to make use of nearly all the potential pollinators of a tropical community. As one of the more primitive families of Tubiflorae this radiation can be presumed to have been accompanied by, and in turn to some extent responsible for, the evolution of such animal specialists as flower bats, hummingbirds, hawkmoths, and long-tongued bees.

2. The majority of species of Panamanian Bignoniaceae are morphologically adapted for pollination by long-tongued bees. These plants have evolved different specializations in flowering phenology which correlate with the different behavioral patterns of their pollinators—steady state flowering with traplining behavior; big bang and multiple bang flowering with opportunistic behavior. Presumably the pollinator behavioral patterns coevolved with the bignon phenological specializations and with similar and concomitant specializations in other plant groups.

3. Among those genera of Bignoniaceae retaining the generalized cornucopia phenology, seasonality of flowering is important in making possible differential utilization of the same group of pollinators by different plant species. From the viewpoint of the pollinator, this seasonal sequence of flowering provides a year-round source of nectar to bignon-visiting pollinators.

The varied and often complex patterns of interaction shown by Bignoniaceae with different animals appear to have long coevolutionary histories. Understanding such interactions promises to be useful in working out evolutionary relationships within the Bignoniaceae. In addition such studies of taxonomically delimited subsets of diverse tropical ecosystems have great potential for elucidating the incredibly complex ecologies of these communities.

LITERATURE CITED

BORRERO, J. I. 1972. Explotación de las flores de Guayacán (*Tabebuia chrysantha*) por varias especies de aves e insectos. Biotropica 4: 28–31.

CROAT, T. B. 1969. Seasonal flowering behavior in Panama. Ann. Missouri Bot. Gard. 56: 295–307.

DUGAND, A. 1942. Dos nuevas Bignoniaceaes del valle del Magdalena. Caldasia 1: 29–35.

FAEGRI, K. & L. VAN DER PIJL. 1966. The Principles of Pollination Ecology. Pergamon, London.

FRANKIE, G. W., H. G. BAKER & P. A. OPLER. 1973. Tropical plant phenology: applications for studies in community ecology. *In* H. Lieth (editor), "Phenology and Seasonal Modeling." Springer-Verlag, Berlin (in press).

GENTRY, A. H. 1969. *Tabebuia* (Bignoniaceae) in Central America. Master's thesis submitted to the University of Wisconsin, Madison.

———. 1972. An Eco-Evolutionary Study of the Bignoniaceae of Southern Central America. Ph.D. thesis submitted to Washington University, St. Louis.

———. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica. 6: 64–68.

HARRIS, B. J. & H. G. BAKER. 1958. Pollination of *Kigelia africana* Benth. Jour. West Afr. Sci. Assoc. 4: 25–30.

HEINRICH, B. & P. H. RAVEN. 1972. Energetics and pollination ecology. Science 176: 597–602.

JANZEN, D. H. 1967*a*. Synchronization of sexual reproduction of trees within the dry seain Central America. Evolution 21: 620–637.

———. 1967*b*. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Univ. Kansas Sci. Bull. 47: 315–558.

———. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171: 203–205.

———. 1972. Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest. Ecology 53: 885–892.

LEWIS, W. H. 1971. Selective insect damage in a tropical herbarium collection. Ann. Missouri Bot. Gard. 58: 91–92.

LINDLEY, J. 1847. The Vegetable Kingdom. London.

PIJL, L. VAN DER. 1956. Remarks on pollination by bats in the genera *Freycinitia*, *Duabanga* and *Haplophragma*, and on chiropterophily in general. Acta Bot. Neerl. 5: 135–144.

RECORD, S. J. & R. W. HESS. 1940. American timbers of the family Bignoniaceae. Tropical Woods 63: 9–38.

SANDERMANN, V. W. & H. H. DIETRICHS. 1957. Untersuchungen über termitenrisistente Hölzer. Holz als Roh- und Werkstoff 15: 281–297.

SCHULZ, A. G. 1940. Las Bignoniaceas del Territorio del Chaco. Lilloa 5: 131–158.

SEEMANN, B. 1854. Botany of the Voyage of H.M.S. *Herald*. London.

———. 1860. Synopsis Crescentiacearum: an enumeration of all the Crescentiaceous plants at present known. Trans. Linn. Soc. 23: 1–22.

SEIBERT, R. J. 1940. The Bigononiaceae of the Maya area. Carnegie Inst. Washington Publ. 522: 375–434.

SOUTHWELL, C. R. & J. D. BULTMAN. 1971. Marine borer resistance of untreated woods over long periods of immersion in tropical waters. Biotropica 3: 81–107.

STANDLEY, P. C. 1928. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: 1–416.

——— & L. O. WILLIAMS. 1974. Bignoniaceae. *In* "Flora of Guatemala." Fieldiana Bot. 24(10): 153–232.